"SCIENCE OF LIFE" SERIES

HOW ANIMALS BEHAVE

BY

H. G. WELLS

JULIAN HUXLEY

G. P. WELLS

THE
OUTLINE OF HISTORY

BY

H. G. WELLS

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The Seventh Volume in the *Science of Life* Series

WITH ILLUSTRATIONS BY

L. R. BRIGHTWELL

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PREFACE

BIOLOGY is the science of living things. It is a rapidly expanding science, which has now grown so large that it is beginning to divide itself into a number of daughter-sciences.

With this increasing subdivision there comes a tendency for the latest results in the various fields to be known only to specialists, although they may be full of interest and meaning for the lay reader. From each of the different branches he can gather something of consequence if the main results are made accessible to him by being shorn of confusing technical complications. From Systematic Zoology and Botany he can obtain a view of all the different kinds of living things, and of the relations which they bear to each other. From Anatomy and Physiology he can derive an understanding of his body. From a study of Embryology and Reproduction, he can understand his development and his relation to the stream of life. Genetics, a subject of comparatively recent growth, is emerging from a controversial period and is now able to present to him the main principles of heredity with considerable certainty. Evolutionary Biology can trace the actual history of the various forms of life, and in so doing it explains much that is perplexing in their structure and working. Ecology, another recently developed field, is concerned with the different living species, not in isolation, but as interrelated parts of a single web of life; already it has produced results of great service to the breeder and cultivator. Medicine, once the study of diseases, is becoming the study of health. Psychology, in its widest sense, treats of the most fascinating problem of all—

it is just beginning to explain the working and evoluton of mind, from its dim origins to its strange and often devious workings in the culminating human species. Any one of these sciences can be studied independently of the rest, but they all interact and illuminate each other.

This volume deals with one only of the many branches of biology. It is in all essentials complete in itself, and can be read as a single treatise.

But it also forms part of a more ambitious project—*The Science of Life*—which aims at presenting, for the lay reader, a complete survey of the main results of biological science. This work was originally published as a single volume. In preparing the present edition the text has been divided into nine separate volumes, each complete in itself and each dealing with one particular division of biology. The opportunity has been taken to correct errors in the text and to bring it up to date. Together the nine volumes form an integrated whole. Accordingly, here and there in this volume, the reader will find references to others. These cross references indicate passages in which the topic under review links on to other subjects. In no case are they essential to the understanding of the argument of the separate volume in which they occur. But the reader interested in heredity, for example, will find that the subject is intimately linked with evolution; while one who is studying the past history of life is likely to discover that this would become still more interesting if he were to have some knowledge of physiology and of animal behaviour. Those who desire to pursue such clues must do so in other volumes of the series.

We hope that this method of making volumes on separate subjects available singly, while at the same time providing the possibility of a more general view in the series as a whole, will prove satisfactory both to readers who propose to concentrate on a single field and to those who have the ambition to study the whole subject of biological science.

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HOW ANIMALS BEHAVE

CHAPTER I

RUDIMENTS OF BEHAVIOUR

§ 1

The Three Elements of Behaviour

LIVING things act of themselves, and they act discriminatingly and not merely according to the laws that govern the movements of lifeless matter. As we study their activities, we shall find creeping in by almost imperceptible degrees the persuasion that living things do not merely move spontaneously, but feel. As we ascend the scale of being we shall find movements more and more suggestive not merely of feeling but of perceptions, observations, and thoughts as we know them in our own minds. A point will come when we shall have to abandon exterior observation and turn our minds inward for light upon the problems of animal behaviour.

All living things respond to their surroundings. Even the simplest microscopic animals will pursue their prey and

avoid hostile influences; even a plant pushes its roots towards moisture and its leaves towards the sun. All through the spectacle of life we perceive that adjustment of activities to circumstances of which our own triangle of feeling, thinking, and doing is only the culminating case. To this apparently spontaneous adjustment we are now to give our attention.

It may be well to insist upon a possible danger in our treatment of this question, the assumption, which may be either premature or quite wrong, that amœba really feels the influences, such as harmful chemical substances or excessive heat, which it avoids, or that a plant is aware of moisture and light, and responds to them in a way which involves some sort of parallel to our own consciously appreciated feelings and responses. There is only one conscious mind (the point is too often made in abstract discussions to need further elaboration here) of whose existence a man may be sure, and that is his own. His belief in the existence of other similar minds in his friends and acquaintances, rests only upon inference. Their acts and speech, and general similarity to himself, force him to that conclusion. When he considers creatures of other kinds the same inference follows the same observation; the behaviour of his dog at a pleasing or a disappointing event recalls in many ways that of his child under similar circumstances, and presumably betokens the same joy or sorrow. Perhaps he reads a similar mental life, albeit at a lower level, into frogs and fishes, and even invertebrate animals. That is the tendency. But let us be on our guard. To read a consciousness like our own into a creature so elementary as an amœba simply because it shrinks at a harmful stimulus is intellectually dangerous; to read a mind like our own into so differently organized a creature as an insect, or a mollusc, is dangerous, too. They may have minds, but as different from our minds as their bodies are from our bodies. In the past the study of the lower creatures has too often been complicated and impeded by such insidious temptations.

Presently we shall study in some detail a little living auto-

maton called the slipper animalcule. It is one of the protozoa or single-celled animals. Can such a creature be said really to feel? We do not know; that depends on whether it has a conscious mind. But external influences, such as warmth of the water, or chemical substances dissolved therein, can act upon the creature and modify its behaviour. Does a slipper animalcule think? Apparently not, since, as we shall see, it lives entirely in the present, and shows no evidence either of memory or forethought. But there is a certain evident adjustment of its acts to its circumstances. The sudden impact when it runs up against a hard obstacle is met by an avoiding reaction, but at the different touch of a mass of the bacteria upon which it feeds the animal stops and begins to eat.

To review the whole range of behaving life we shall find it best to consider our matter under three aspects. First, there is receptivity; organisms can be influenced by external circumstances. This in ourselves is often (but not always) accompanied by sensation. Second, there is activity; organisms swim, or run, or grow, or blush, or perspire, or perform any of a multitude of apparently spontaneous acts. Third, there is correlation; the acts are more or less accurately suited to the circumstances, and the whole of the machinery of this fitting of the one to the other, ranging from the simplest automatism to Everyman's conscious and deliberate thought-processes, we treat under this third head.

It will make the matter plainer if we take these heads one by one, and see how in each case the first organized beginnings lead up to the state of affairs found in ourselves.

§ 2

Receptivity

The frog is so constructed that its brain and spinal cord can be destroyed with a needle in less time than it takes to hang or electrocute a man. For this reason, besides its

commonness and general availability, it is one of the most-used laboratory animals.

Suppose that we have a frog which has been "pithed" in this way—the brain and mind destroyed, the heart, abdominal organs and so forth still living—and that we remove from it the calf-muscle with its attached nerve. They lie limply on the experimental table. The muscle is pink and spindle-shaped and about an inch long. Before its removal it was firmly attached at its upper end to the bones at the knee, while below it tapered away into a glistening tendon—a tough, flat ribbon of tissue which ran round the heel to the sole of the foot. Most of the tendon and a fragment of bone from the knee have been taken out with the muscle. The nerve is a white, slender, living string, and an inch or so of it is still attached to the muscle.

These organs can retain their vitality for hours if they are properly tended. They are kept reasonably cool, and moistened from time to time with a little of a properly mixed salt-solution.

If we pinch the muscle or press on it, it will suddenly quiver and shorten; the same effect may be produced by giving it a weak electric shock, or by adding a drop of an appropriate chemical solution. In biological language, the muscle is said to be "irritable" or "excitable," and the pinch or electric shock or chemical agent by which we can make it move is called a "stimulus." A fraction of a second after the stimulus the contraction passes off and the muscle lies limp as before, so that we can repeat the experiment again and again.

The nerve also is irritable, but its activity manifests itself in another way. Its rôle in the organism is not to contract but to conduct. So, when we pinch it or otherwise stimulate it at any point, it shows no outward sign of change, but the muscle to which it is attached abruptly shortens, as if in response to direct stimulation. Our experiment simply sent impulses flying along the nerve from the point we stimu-

lated, and those impulses, reaching the muscle, stimulated it in its turn to activity.

The impulses in the nerve are invisible, but they can be detected electrically. If we connect to some part of the nerve a delicate apparatus for recording very slight electric currents, and then stimulate another part of the nerve, we should see a little tremor of the recording apparatus a fraction of a second after the stimulus, as the impulses flashed by on their way down the nerve.

Here we have a very simple demonstration of irritability, which is one of the most fundamental properties of living substance; and if it has been set forth in a manner somewhat recalling the elementary class-room, the triplex author pleads the importance of the phenomenon as his excuse. Irritability is a universal property of protoplasm, and without it there would be no sensation, no consciousness, no nervous activity. The whole harmony of the body, the whole of the matter with which this Volume is concerned, depends upon it.

The rich variety of sense-organs with which our bodies are provided were reviewed in the first Volume of this Series, *The Living Body*. They show a very considerable diversity of structure and working. The man in the street speaks of the evidence of his five senses; to the biologist this is undue modesty, for in actual fact (allowing for the different kinds of skin sense, internal sense, and so on) he can give a list of about twenty.

We watch the isolated muscle as it twitches at our bidding on the table before us; at first sight the relatedness of the two processes, its twitching and our watching, is not apparent. But related they are. The working of a sense-organ is no more than a refinement and a specialization of the irritability of an isolated muscle or nerve.

Consider what we have already learnt. The frog's muscle can be stimulated by a pinch or a light jolt. In our bodies there are various kinds of cells (or parts of cells) which specialize in extra sensibility to such mechanical stimu-

lation. Wrapped round the sheath that encloses the root of a hair, they underlie one of the most delicate forms of touch. Grouped at the openings of the semicircular canals into the main cavity of the inner ear, they tell us how our heads are moving. Arranged in a row along the spiral chambers of the cochlea, they enable us to hear and to distinguish notes of different pitch. The essential nature of the response is in all cases the same; but its meaning to the organism depends on the situation of the touch-sensitive organs, on the special construction of the parts where they are placed. In the course of evolution this fundamental property of mechanical irritability has been seized upon and turned to a variety of uses.

To make the idea plainer, let us take another example; let us watch Nature at work and trace stage by stage how out of a generalized irritability she builds that marvel of organic engineering, the human eye.

Light can be shown to have a direct stimulating action on undifferentiated protoplasm. A beam of intense light focused on to one end of an Amœba causes, first a local contraction of the stimulated region, and then movements of the other parts, which lead to the animal's crawling out of our experimental limelight. Very strong light suddenly flooded on to the whole animal makes it contract and draw itself together into a rounded blob, and may paralyse and even kill it. From such crude light-sensitivity as this we start our story.

The second step is found in other protozoa, where part of the body is specially irritable. The front end of the ciliate Stentor, for instance, is considerably more sensitive to light than the rest; and the animal shows the curious reaction that whenever the illumination of this delicate front end is suddenly brightened it abruptly reverses its direction and swims backward for a short distance, then twists round a little so that its front end points a new way, then goes forward again. This behaviour has a definite value. If we put a number of Stentor into a glass dish, fairly brightly

FIG. 1.—THE MICROSCOPIC, SHAPELESS, FLUID BODY OF AMŒBA, WHICH, ALTHOUGH IT HAS NO SPECIAL SIGHT-ORGANS, SHOWS A PRIMITIVE SENSIBILITY TO LIGHT.

(Photo by H. Bastin.)

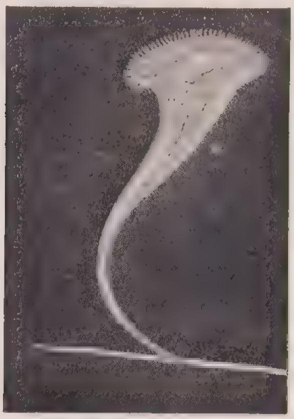


FIG. 2.—STENTOR, ANOTHER PROTOZOON WHICH IS SENSITIVE TO LIGHT.

It can anchor itself to a fragment of pond-weed, as shown, or swim about in the water.

(Photo by H. Bastin.)

illuminated, but with a patch of shadow in it, the animals will be found in a little time to have collected in the shade. If now we watch them through a microscope as they swim about, we shall see that every now and then one of them gets to the edge of the shadow; but as soon as its sensitive pole feels the bright direct light of the sun, the animal gives its "avoiding reaction," backing abruptly and changing direction, and thus keeps in the shade. Moreover, when it is outside, in a bright light, the animal only swims straight when its front end lies in its own shadow, i.e. when it has its back to the light; if it is pointing in any other direction it twists about, apparently at random, until this position is achieved. This reaction will evidently guide it automatically out of open sunlit waters to shady corners.

An opposite reaction to light is shown by those protozoa which have simple plants living in symbiotic partnership inside them. The common slipper animalcule, *Paramecium caudatum*, a creature found in stagnant pools containing decaying leaves and the like, neither seeks nor avoids light unless it be so very intense as to be injurious. But its close relative, *Paramecium bursaria*, which contains algæ, swims towards the light and therefore collects near the surface of the water, where its green partners can build up starch and sugar most effectively.

In many protozoa there are special structures called eye-spots—usually red in colour—and it would appear that they are involved in some way in the animal's responses to light. But just how they act has not yet been made clear.

In these simple creatures, then, we get something we may call a light-sense; but it is not one that can be legitimately described as sight. It does not involve any sort of image-formation whatever. The animals are by our standards blind. They are unable to see other objects. They simply behave in a certain fashion when they are illuminated to a certain degree of brightness. If these single-celled bodies can be said to feel at all, then they feel light as a sensation more like our own somewhat vague perception of the

warmth of a fire than our seeing it—or like the sense of illumination we get when we lie sun-bathing and the sun beats down on our closed eyelids. They do not look *at* things, much less do they look *for* things; they simply respond to the degree of illumination. In this way Stentor finds a shady corner, while *Paramecium bursaria* comes out into the light.

To see in the proper sense of the word—to focus and form images of distant objects—demands a more complicated eye than can possibly be fitted into a protozoan body.

Among many-celled creatures, there are a number which show a "light-sense" no higher than that of protozoa. Earthworms are sensitive to a bright light and crawl away from it, but you can dissect an earthworm as minutely as you will, and find no trace of eyes. The organs responsible are single isolated cells of a rather curious kind, which lie scattered about all over the skin, in among the other cells of the epidermis. Similar diffusely sprinkled light-sensitive cells are known in a great number of forms. Tadpoles apparently feel light over their whole skins; if after a tadpole has been blinded it is put in the dark and then suddenly illuminated, it begins to swim actively about—which shows that the light must act as a stimulus on its skin. The lancelet, *Amphioxus*, has light-feeling cells in a curious place—buried in the nervous substance of its spinal cord; because of its thinness and translucence the whole of its anatomy is illuminated, and a light-cell inside is pretty nearly as useful as one on the skin.

In these cases, of course, we are no more justified in speaking of sight than we are in the case of the protozoa. It is doubtful if we may even speak of feeling. The earthworm lies out of its burrow before dawn, feeding on dead leaves and the like; as the sun rises and shines on it, it retreats into its burrow. That is about all its light-cells can do for it. It does not see the early bird approaching; but with reasonable luck (and with its great sensitivity to even the slightest jarring of the earth, as stand-by), its light-sense will guide it to safety as its enemy begins to stir.

The next great step in the evolution of sight is the collection of the scattered sight-cells together into primitive eyes. Fig. 3 shows three types, such as are found in a great number of invertebrate animals. In each drawing the skin of the animal is supposed to be cut across and magnified; the conspicuous palisade of cells being the epidermis, separating the rest of the animal below from the outer world above. The sense-cells are gathered together into patches, and at their inner ends they send nerve-fibres down to a brain. In the uppermost eye the sensitive bit of skin (which is thicker than the rest) bulges slightly outwards, and there is a copious deposit of black pigment (shown stippled) between the cells. In effect, this pigment forms a black tube round each sensitive cell, so that the latter is only strongly excited by light that falls upon it in the direction in which it points. So in this very simple kind of eye there is a sort of crude image formation. The creature distinguishes when there is something pale or luminous in one direction and something dark in another, and is perhaps aroused by conspicuously moving objects—although this sort of vision must be at the best hazy and without definite outlines. Such eyes as this are found in a number of worms and other lowly organized invertebrates. They are, of course, very small, and appear simply as little specks of colour on the head, horns or other parts of their possessors.

The eyes in the middle and lower part of our figure show a different tendency; here the sensitive surface is curved inwards instead of outwards. But pigment between the cells serves the same purpose as formerly. Here, however, we note the first rudiments of an additional refinement—a device for concentrating and perhaps focusing light. In the middle eye the elementary retina has been dimpled in to form a definite cup, and inside the cup there is a special glassy substance secreted by the cells themselves. This state of affairs is found in many jelly-fishes, star-fishes, and worms. The eyes of a limpet are of this kind, but those of its more familiar relative, the snail, are more complicated. In the

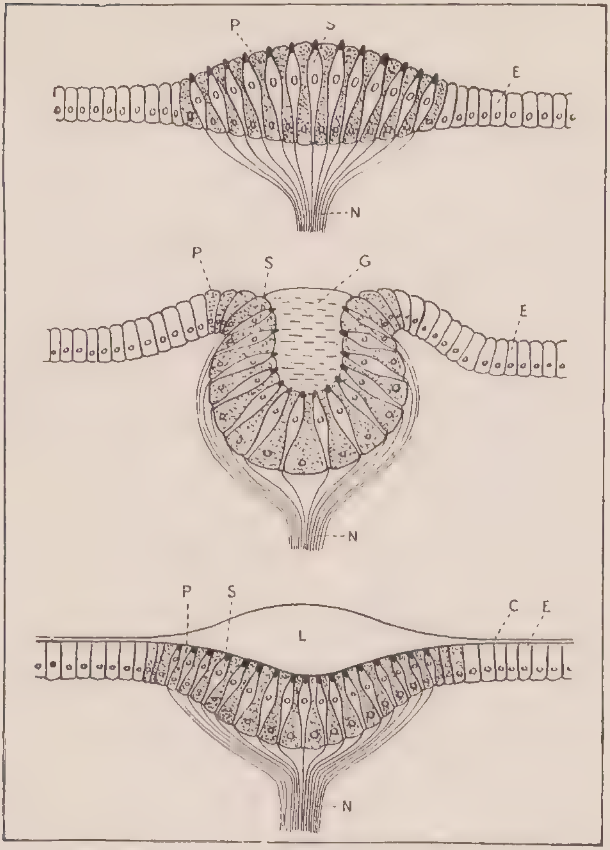


Fig. 3.—Three Simple Kinds of Eye, as described in the Text.

(E) Cells of skin. (S) Cells sensitive to light. (P) Cells full of black pigment. (N) Nerve fibres. (G) Glassy substance exuded by the cells. (C) Cuticle. (L) Lens.

eye at the bottom of our figure the retina is less markedly curved, and here part of the cuticle (a thin, hard, transparent layer of secretion that covers the body in most invertebrates) is thickened to form a primitive kind of lens. This last arrangement, with various minor complications, is found in other members of the groups just named, and in molluscs and the primitive worm-like arthropod Peripatus.

In these three kinds of sense-organ, primitive and inefficient though they be, we can discern the two fundamental features of true eye-construction. The first is the presence of protoplasm which is specially sensitive to light.[1] This localization first appeared in our account with Stentor, and we trace it through the light-feeling cells of earthworms to these elementary eyes. The second is the grouping of a number of these cells into a working unit; and it is this which makes true seeing possible. Each cell corresponds to a particular direction from which light-rays may come. It corresponds, so to speak, to a sector of the environment. So between them, taken together, the cells form a spatial image. Not until such an arrangement as this had been evolved could the shapes and movements of distant objects be perceived and influence an animal's behaviour.

There we have the essentials of the evolution from mere light-irritability to sight. To attain to the clear vision of a bird or a higher mammal is only a matter of perfection of detail. We can note some of the main steps, although it would not be worth our while to go into all the minutiæ of the process. The story is complicated by the fact that the invention and gradual elaboration of the eye have gone on independently in a number of groups, sometimes along parallel lines and sometimes in strikingly different ways.

[1] Our own retinal cells are not directly stimulated by light, but by a chemical substance produced when light falls on the retina. How far this is general is not yet clear, for the discovery is a recent one, but in the diffuse light-cells of a sea-squirt (which are like those of earthworms discussed above) it has been shown that stimulation has also a chemical basis. Whether this is also true of protozoa and of the light sensitivity of undifferentiated protoplasm is not yet known.

From the hollow kind of eye shown in the middle and at the bottom in Fig. 3 we can lead up to eyes like our own. First the sensitive dimple of skin pinches itself off altogether from the rest and comes to lie a little way below the body surface in the shape of a hollow ball. Then the optical

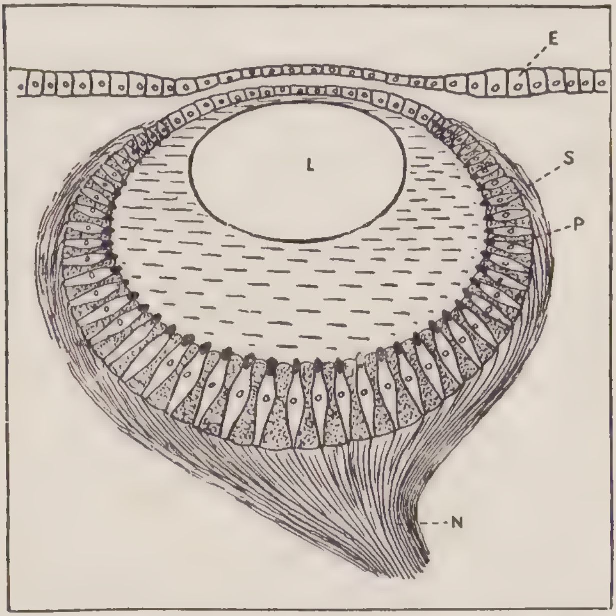


FIG. 4.—A FURTHER STAGE IN THE EVOLUTION OF THE CAMERA EYE (SEE TEXT).

The parts are lettered to correspond with those in Fig. 3.

apparatus is improved and extended. In some molluscs and worms this is done by specializing part of the glassy substance inside the eyeball as a more or less spherical lens; in this case only the deep half of the eyeball is sensitive to light, the side lying against the skin, and the skin itself, being transparent to admit as much light as possible. Fig. 4 shows an eye of this kind. In other cases, such as the third eye

FIG. 5.—THE CAMERA EYE.

FIG. 6.—THE CAMERA EYE.

in the middle of the forehead with which our reptilian ancestors were provided, the outer wall of the eyeball itself forms a lens. Or the lens may be made out of the skin over the eyeball; this is what happens in ourselves and in a number of the higher molluscs.

Thus the retina and the lens arise. Similarly, we can

FIG. 7.—THE CAMERA EYE.

FIGS. 5, 6, 7.—THE THREE CLIMAXES OF THE CAMERA EYE.
The eyes of birds of prey are remarkable for clear vision at a distance. Those of monkeys and men are unique in having a "yellow spot" on the retina; also they are placed side by side to allow of stereoscopic vision. (*Photos by H. Bastin.*) Those of octopuses and cuttle-fish, although independently evolved, show striking parallels with the eyes of vertebrates. (*Photo by W. S. Berridge.*)

trace further elaborations—the cornea and iris, the appearance of muscles to focus the eye on objects at various distances, the gradual refinement of the structure of the retina itself, culminating in the yellow spot of monkeys and men.

It is fascinating to note that a parallel evolution has taken place in those highly organized molluscs, the octopuses and cuttle-fish. A comparison of Fig. 9 with a diagram of a human eye will show how closely the cephalopod eye, with lens and cornea, iris and focusing-muscles, resembles our own. Nowhere else among the invertebrates has such perfection of detail been evolved—at least not in an eye of this kind.

But there is another, very different, direction in which the eye has evolved. We may call the type which culminates

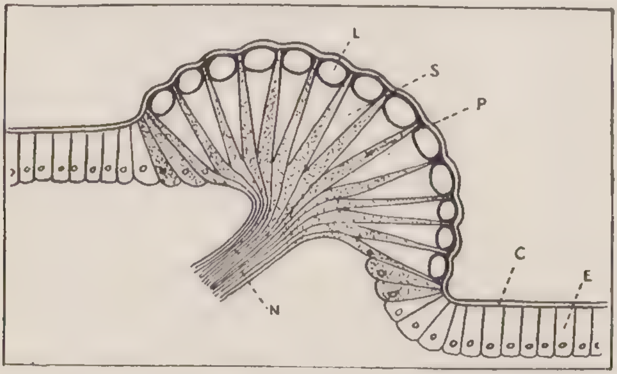


Fig. 8.—An Early Stage in the Evolution of the Compound Eye—the Eye of the Tube-worm lettered to correspond with Fig. 3.

in octopus, vulture, and man the camera eye. But the primitive convex type shown at the top in Fig. 3 contains other possibilities, which are worth tracing as they develop stage by stage.

There are some marine worms which live in tubes they build out of sand or fine gravel, spreading a crown of feathery tentacles to catch minute particles of food. Many of these worms have simple eyes on the tips of their tentacles, and Fig. 8 shows one of these eyes cut across. It is like the uppermost eye of Fig. 3, but it shows an improvement in that each of the sensitive cells is provided with a tiny light-

concentrating lens of its own. Each is in fact a miniature unit eye. Because of their convex grouping each of the eye-cells looks out in a slightly different direction from the others, and between them they build up a kind of mosaic picture of the surrounding world. Each by itself is unable to make an image, since it has only a single nerve-fibre; it

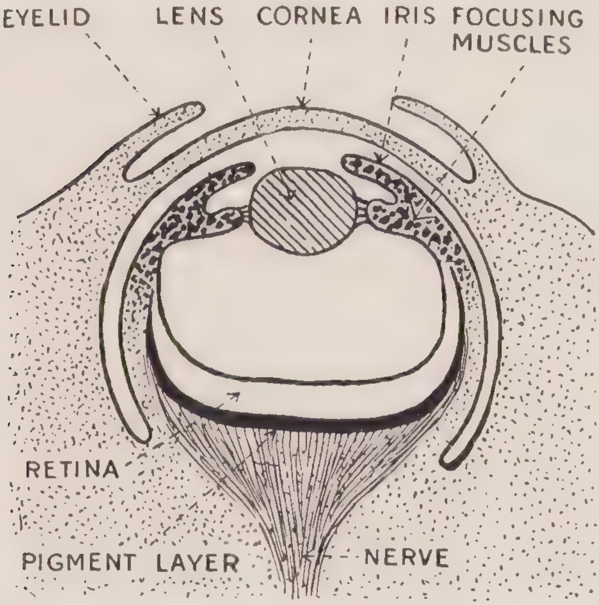


Fig. 9.—The Eye of a Cuttle-fish cut across, for comparison with the Human Eye shown in Fig. 47, of Vol. I, The Living Body.

simply telegraphs to the brain: "I am receiving light"; "I am not receiving light," with additional comments, perhaps, on the intensity and colour. The image synthesized in the brain is a mosaic of all these separate units of information, much as a weather-chart is built up from the reports of local meteorological stations.

This is how we may suppose the eye of the tube-worm to act. But, oddly enough, there is no direct evidence that the creature forms images in this way. So far as we know it only shows one kind of reaction to light, and that is a very simple one. Whenever the light falling upon the worm is suddenly dimmed, it flicks back with lightning speed into its tube. A passing shadow will do it. The value of this "shading reaction" to the organism is too plain to need stressing; one has only to think of a fish browsing over the sea-bottom in search of attractive morsels to snap up. Moreover, the reaction is obviously a very simple one—as simple as the avoiding reaction given by Stentor when suddenly illuminated. Similar reactions to a passing shadow are seen in a great number of sluggish and sessile shore-creatures. While these worms snap back into their tubes almost too fast to see, barnacles close their shells abruptly; many sea-squirts contract up into gelatinous blobs; burrowing bivalves withdraw their soft, protruding siphons into the sand. Sea-urchins cannot withdraw into safety; in some of them, however, sudden shading causes them to bristle up their spines, and if the shading is only partial the spines turn towards the shaded spot. Thus, as our browsing fish prowls along with his tell-tale shadow sliding beneath him, the invertebrate world hides or arms itself at his approach.

Many of these creatures are eyeless; and whether the comparatively well-formed eyes of a tube-worm are really used only for this purpose, or whether they provide the owner with a further crude visual power that has not yet been detected, we cannot say. But we must return to our evolutionary story.

Eyes like this one that we have been describing, but with various extra complications, are found in one or two bivalve molluscs, where presumably they have been independently evolved. But the type reaches its highest development in the astonishing compound eyes of arthropods. If magnified some eight or ten times, the head of a dragon-fly shows most of its surface covered with an enormous pair of faceted eyes

—each eye a multitude of crowded eyelets, each eyelet a somewhat more complicated version of the single eyelets seen in the tube-worm.

Thus, stage by stage, and in various directions, the eye has evolved; thus a primitive vague awareness of light has been elaborated and refined into sight as we know it. We could trace other stories like this one; for in the same sort of way the sensibility of the lowest animals to warmth or cold, to a touch or a jar, to various chemical substances has been specialized in higher creatures to serve a multitude of purposes. By insensible degrees we pass from a primary sort of receptivity that is like the purely mechanical irritability of an electric bell-push, to a discriminating reaction that is indistinguishable from our own seeing. Vitalists like Bergson have made a tremendous difficulty about the evolution of the eye, declaring it is too complicated a process for unassisted natural selection. But is it after all so inexplicable?

§ 3

Response

As every reader knows, Everyman's movements are brought about by muscles. Of these he has several kinds. There are the "voluntary muscles," by means of which he performs deliberate movements; there are the "involuntary muscles" in his intestines, heart, and so forth, that behave independently of his will. These two kinds of muscles can be distinguished by their microscopic structure and by their physiological properties. The involuntary muscles only come into action at the call of impulses from the central nervous system, but when they do so they contract with great promptitude and vigour. The involuntary muscles are independently active, but they work more slowly and feebly. But the line between the two is by no means sharp. Heart muscle combines many of the features of such muscle as that found in the walls of the stomach with others of the

voluntary muscles. Muscle from that strange almost molluscan organ, the tongue, is in some ways intermediate between other voluntary muscle and heart muscle. When we take other animals into account, the number of kinds of muscle becomes very great indeed.

Now, just as the responsiveness of our sense-organs is no more than a specialization of protoplasmic irritability, so the shortening and relaxation of our muscles is no more than a specialization of a general power which living substance has of changing its shape. We have already dealt with the slow, flowing movements of Amœba, which can bulge out its shapeless body into a protruding lobe in whatever direction it pleases. Related to this, it would seem, are the restless, flowing movements of other cells—such, for example, as the endless circulation of the protoplasm of many plant cells round the tiny boxes of cellulose in which they are imprisoned. In recent years Pantin has shown, at Plymouth, that the movements of an Amœba have many properties in common with the movements of a muscle-cell ; the two are similar in their relation to oxygen-lack, to temperature, and to a great number of chemical substances. In brief, a muscle-fibre is a cell specialized in such a way that this primitive contractility of living material is made vigorous and efficient.

In another direction, we can trace a series of intermediate stages in one creature and another, leading from the flowing, temporary lobes of Amœba to the delicate vibrating filaments called cilia or flagella—found, for instance, in many protozoa, in spermatozoa, and in various other kinds of animal and plant cells. Here, again, a recent piece of work by Gray, at Cambridge, has shown that cilia have the same fundamental mechanism as muscle.

But movement is not the only way in which an animal can respond to environment. Everyman may change colour at a sudden surprise ; he may even break out into a cold sweat. His colour change is, of course, a change in the amount of blood in his skin, and is really only a disguised

kind of muscular movement, for it depends on the contractility of muscles or muscle-like elements in the walls of his blood-vessels. But perspiration depends on glands, not muscles. Similarly, if something has delayed his meal, his mouth may water at the sound of a dinner-gong from a neighbouring house. Here, also, he responds to the stimulus by secretion. We, ourselves, like most vertebrates, are predominantly muscular animals, and glands play a comparatively small part in our external behaviour. For clear examples we must turn elsewhere. If you take a newt out of water and handle it, it will exude a clear, slimy secretion over its whole skin to make itself slippery and help in wriggling out of your hand. If you treat it too roughly or hold it too long it will exude another kind of fluid—less transparent and less oily to the touch, but containing an irritating poison. A lady who tried the experiment of gently biting the tail of the crested newt—the larger of the two common English newts—reported a bitter, astringent taste, irritation of the throat, a strong flow of foamy saliva, violent automatic movements of the muscles of the mouth, and a headache that lasted for several hours.

Many other amphibians show a similar power of responsive exudation; indeed, the highly glandular skin is as distinctive of amphibians as is the scaly skin of reptiles, the hairy skin of mammals, or the feathered skin of birds. The poison glands cluster very thickly in the warts with which the skin of a toad is beset; and anybody who has seen a dog take a toad in its mouth knows that they can be used to advantage. Their action on ourselves results in symptoms not unlike the early stages of a cold in the head. According to report, the Colombian tree-frog, *Dendrobates tinctorius*, has so venomous a secretion that the Indians use it for poisoning their arrows; one frog held over a fire (and this species seldom exceeds an inch and a half in length) pours out enough for fifty arrow-heads. In this case the poison acts chiefly on the nervous system. Snails provide a well-known example of defensive secretion; everybody knows

how an irritated snail will retire into its shell and exude a quantity of frothy slime.

Many fishes possess a silvery internal organ called a swim-bladder or gas-bladder. Apparently they have the power, by means of a special gland, of secreting gas into the bladder and so regulating their density according to the depth at which they are swimming.

A special kind of secretion is the formation of luminous substances—a property which is surprisingly widespread in the animal kingdom. As anybody knows who has taken a row-boat or a canoe on the sea on a summer night, the surface waters abound in tiny organisms which give out flashes of white or greenish light when they are alarmed; the sea seems to light up at every stroke of the paddle. In a number of nocturnal animals light-producing organs are used to attract the notice of the other sex. In fire-flies the various species have characteristic rhythms which they flash out as they fly, much as grasshoppers have distinctive rhythms in their chirping.

Sometimes the light-producing organs are simple glands, no more complicated than the skin glands of newts and toads; but in other cases (such as deep-sea fish) there may be elaborate accessories—reflectors behind, and even lenses in front, so that the light shines out in a definite beam.

Clearly, the variety and degrees of organization of different kinds of responsive tissue are considerable. In what follows we shall need a word to cover all these various responsive tissues and structures—muscles, cilia, glands, and the other organs that we are about to discuss. The most convenient word for the purpose is "effector." A muscle-fibre is one kind of effector; a gland-cell is another.

As a further kind of response, we may note the changes of colour of chameleons, frogs, and flat-fish and the even swifter changes of octopuses and their relatives. In the latter case the colour-change is really only a kind of muscular movement. If you look carefully at the skin of a living octopus in an aquarium, you will see that the pigment is

not diffused uniformly but gathered into definite specks. These specks can expand or shrink, and thus darkening or paling of the whole skin is brought about. Each speck is really a tiny elastic bag containing pigment, and it is attached to a number of muscle fibres which radiate away from it through the skin. When the muscle-fibres contract they pull on the bag from all sides and it expands; when they relax it shrinks again because of its elasticity.

But the colour-changes of other creatures are less prompt and vigorous, and due to effectors of a different kind. Here the pigment-cells are branched, radiating structures, and the pigment inside them can either spread through the whole cell (producing darkening of the skin), or collect into a tight little speck in the middle (producing paleness). Recent experimental work suggests that these cells are modified contractile cells, and fit into the movement-producing group that we discussed above.

But perhaps the strangest effector of all is seen in certain fish, which can give electric shocks to any other animals that happen to come into their immediate neighbourhood. Many of the common skates and rays have living batteries at the roots of their tails; if you grasp them at that point they can give you a shock of about a volt, or about half the voltage of an ordinary pocket flash-lamp battery. In the aquarium at Monaco you can, for a small fee, make the experiment of touching the Mediterranean electric ray, *Torpedo marmorata*, which has stronger batteries at the sides of its body. If it is feeling vigorous, and if you have not had too many predecessors, it will give you some twenty or thirty volts. One or two other kinds of electric fish can do better than this. Strongest of all is the electric eel, a fresh-water fish from South America. This animal, which may be five feet long, has a powerful battery running the whole length of its body, and accounting for more than a third of its weight; it can give you a shock even if you handle it in a surgeon's rubber gloves, its potential reaching several hundred volts (more than the voltage of domestic

electric light). Frogs and little fish can be electrocuted at once by the electric eel.

In most cases at least, these electric organs are modified muscles. The normal activity of a muscle is accompanied by slight, incidental electric changes; and in the electric fishes, Nature has seized upon this fact and modified the muscle-cells until their power of shortening is lost altogether, while the electric currents they produce are intensified. Each of these modified muscle-fibres has the shape of a thin plate of tissue and an electric organ consists of a great number of these plates, put together like a pile of pennies, with their separate electrical effects summing up, just as ordinary dry-cells sum up if they are connected in series. The electric eel has about seven thousand of these living electric cells in series with one another on each side of its body, all ready to work at the bidding of the central nervous system.

These electric organs afford one of the best examples of parallel evolution, for they have been evolved independently in several groups of fishes, now as a modification of one muscle and now of another. In the electric eel and in the common skates and rays part of the column of muscle that runs along the whole trunk and tail, and performs the swimming movements, has been converted to this new use. In the electric rays, or "torpedoes," a muscle that generally lies close to the skin and wraps round the gill region has been "electrified," and lies as a large, white cake-like body on each side of the fish. In a recently discovered electric fish, *Astroscopus*, which is related to the perch and stickleback, the battery lies just behind the eye, in a cavity that pouches off from the orbit. Also—oddly enough—it is supplied by a branch from one of the nerves to the muscles which move the eyeball; so it looks as if the battery itself is a specialized part of one of the muscles that roll the eyes.

But the strangest case of all is found in the electric catfish, *Malapterurus*, from African rivers. Here the batteries lie actually in the skin and form a blanket round most of the body. Moreover, they are supplied by two nerve-fibres

only, one on either side of the animal. In this case, the organ is apparently not a modified muscle at all, but a modification of the glands of the skin. It has been shown that in ordinary glands (such as the salivary glands), activity is accompanied, as in muscles, by slight electrical changes. So Nature can make her living batteries from two quite different kinds of raw material.

§ 4

Correlation : the Origins of the Nervous System

As we ascend the scale of life we discover a more and more elaborate co-ordination of receptivity and response.

A nerve is a sort of living telephone wire, and the central nervous mass made up of brain and spinal cord is like a telephone exchange. Nervous messages flash up from the sense-organs along nerves, and, also along nerves, outward messages flash down to muscles, glands, and so on. In the central nervous mass the sensory messages are weighed and integrated ; decisions are made ; appropriate commands are dispatched that result in action.

Now the simplest living creatures have none of these organs. How, in them, is action suited to sensation ? Can we discern the rudiments in an Amœba of our own nervous activity, as we have already discerned the rudiments of our sensibility and muscular movements ?

The whole surface of an Amœba's body, we noticed, is equally sensitive to various stimuli such as heat, strong light, harmful chemicals, or the neighbourhood of food.

The whole surface is contractile, and every part can be protruded as a temporary limb, or can form an improvised mouth or anus. Similarly its whole body can conduct impulses from a stimulated spot to other parts at the rate of a small fraction of an inch per second. This slow, sluggish communication between part and part is the primitive type of co-ordination from which the vastly more rapid and

efficient conduction along our own nerve-fibres has been evolved. It is, like irritability or contractility, a fundamental property of protoplasm. Just as the one property has been refined and specialized in a sense-cell and the other in a muscle-cell, so a nerve-cell is simply a cell which is pulled out into a long, thin thread running from one part of the body to another, and in which this primitive protoplasmic property of transmission of impulses is picked out and made into the primary function.

Amœba, then, has all three of the fundamental elements of behaviour—the reception of stimuli, the transmission or conduction of impulses, and the final action of an effector organ, but all are indiscriminately blended, diffused through the whole body. There lacks the definition of special parts, and since any bit of an Amœba's body may be now a sense-organ, now a nerve, now a muscle, the protoplasm manifests that general inefficiency that one expects from a jack-of-all-trades.

Other protozoa possess a permanent form, and permanent effectors such as cilia or flagella. Much of their behaviour is determined by this structure, for they move with one end forwards, and in particular ways, swiftly or slowly, smoothly or in jerks, in straight lines or spirals, as determined by the arrangement of their cilia. A number have also sense-organs or the beginnings of sense-organs. As we have seen, there may be a zone round the mouth or at the front end which is more sensitive than the rest of the body, and quite frequently there are such special organs as eye-spots.

Finally, in some of those highly organized protozoa, the Ciliates or Infusoria, there are special nerve-like organs, in the form of fibrils which radiate away from the sensitive parts and co-ordinate the movements of the cilia all over the body. In one or two cases there is even a central mass of this substance, acting perhaps like a very simple brain, to which the sensory portions of the system run in, and from which the motor fibrils run out. These fibrils have apparently the same function as nerves, namely that of rapid con-

duction from one spot which is excited to another where action is carried out; but, of course, they are of quite a different origin from real nerves, being all differentiated inside a single cell, while each of our millions of nerve-fibres is an outgrowth from a whole cell. Thus in this respect as in so much else the protozoa, within their minute and single-celled bodies, have anticipated many of the inventions made later and independently by many-celled animals. These devices are therefore not directly ancestral to ours, but interesting parallels at a lower level of organization.

The bodies of the higher animals consist of republics of co-operating cells. In surveying the whole range of living things known to-day, there are to be noted a number of forms on the border-line between the single-celled and the many-celled—there are the flagellates that live in colonies, the simple filamentous algæ and fungi—and these lead up to more highly organized forms. During early evolution there must have been a transition stage when life was experimenting with variable success with such aggregations of cells. On the cellular level there are surprisingly highly organized creatures like the infusorians that we have just discussed; the first many-celled aggregations were very much less individualized than these. A sponge is a multitude of cells, specialized into several co-operating kinds and growing as a whole into a definite and characteristic shape; but the cells still retain a very considerable degree of independence; cut away a bit of a sponge, or pass it through a fine sieve, and it will reorganize itself without difficulty. A polyp, or a flat-worm, or a sea-squirt, although showing a much higher degree of specialization of organs and tissues, still retains the power of reconstitution to an astonishing degree. It would seem that its parts specialize themselves, but not whole-heartedly, keeping a certain potential independence in reserve. Finally, in the most elaborately organized creatures the subordination of the cell-life to the life of the whole is well-nigh complete.

As one would expect, the development of nervous communications between part and part shows a parallel growth from a stage of preliminary experimental inefficiency to its final elaboration.

We have a primitive kind of communication between cell and cell in the microscopic green spheres, each about one-fiftieth of an inch across, of the colonial flagellate Volvox, which consist of hundreds of individual cells embedded in a common mass of jelly. Each of these cells has a pair of lashing flagella, but they all beat in a disciplined way, so that the colony travels with one side always in front. Here the cells are connected together by fine strands of living protoplasm, and we may guess that, nerve-like, these strands convey impulses from cell to cell, and so make possible their co-operation.

The somewhat similar flagellated cells of a sponge are less well disciplined. In normal conditions each beats away, its stroke quite independent of that of its neighbours; and when conditions are unfavourable it stops and draws in its flagellum. Through the gelatinous tissues of the sponge other cells crawl about like Amœbæ and transport food from part to part. As the various cells multiply the sponge as a whole grows. The only reactions which are directly and rapidly adjusted to changes in the outer world are performed by muscle-like rings of specialized cells round the water-canals and the main mouth through which the current is ejected. Under unfavourable conditions (such as shortage of oxygen in the water) these contract and the water-system is temporarily closed. Also there is a crude kind of transmission in the sponge that foreshadows true nervous action. Parker has shown, working with a tube-shaped sponge that grows on the coral-reefs of Bermuda, that an injury near one of the great outward openings is followed after a little time by the closure of the latter. Apparently an impulse of some kind has crept sluggishly through the tissue from injury to opening—not through special nervous tissue, for such is lacking, but through the

general living flesh of the sponge. To such primitive forerunners of nervous activity Parker has applied the term "neuroid transmission."

True nervous tissue appears in the cœlenterates, where it is associated with specialized sense-organs and with sheets and bands of muscle. But it is curiously primitive in its arrangement, which differs strikingly from that of our own nervous systems. Let us choose a jelly-fish to typify this stage.

The body of a jelly-fish, as is well known, is a transparent jelly-like bell, fringed at its edges with stinging tentacles. In the middle of the lower side of the bell is the mouth, surrounded by larger tentacles and generally at the end of a longer or shorter tube, that dangles down like the handle of an umbrella.

Except for feeding movements of the tentacles and mouth, the jelly-fish has only one form of muscular activity, and that is its swimming. A living specimen in an aquarium tank can be seen to beat rhythmically almost like a heart. Each beat consists of a simultaneous contraction of the whole bell, and it has the effect of jerking the animal upwards through the water. After the beat the bell expands again because of its elasticity: the contraction is brought about by a layer of muscles in the bell.

In his admirable *Science from an Easy Chair*, Sir E. Ray Lankester describes the behaviour of a little fresh-water jelly-fish. First it drives itself upwards through the water with a series of powerful contractions of its whole body; then it rests and floats slowly down like a parachute. But as it descends it captures water-fleas and other animals with its tentacles. Because of its transparency, they do not notice the living snare that is sinking down over them. Then it jerks its way up again, then floats down again, and so on.

That upward jerk, a sudden convulsive contraction of the whole bell, is the main activity of the jelly-fish. Sometimes it beats rapidly and sometimes slowly. Sometimes

it rests altogether for a while. But these changes of rhythm are the only variations it can ring on its single swimming movement.

Spaced at equal intervals round the margin of the bell, are eight "marginal bodies," which contain the chief sense-organs of the jelly-fish. Each includes several different structures. First there is an organ which resembles in its design a simplified version of our own inner ears and perhaps underlies a primitive sense of balance. Then there may be a more or less elaborate eye; and it is believed that the marginal bodies are also sensitive to chemical stimulation. In any event, they function as "stimulating" organs: without the impulses flashed by them into the nervous system, the muscles, as we shall see later, would be passive and would not contract.

The nervous system does not lie in definite tracts, or nerves, as ours does, but it consists of a diffuse lacework of nerve-fibres which pervades the whole bell. Round the rim there is a denser ring of nerve-fibres; that is the only special aggregation of nervous tissue the jelly-fish possesses, the only thing about it that even remotely suggests a brain. As a matter of fact, it is more like a circular nerve than a brain, for it is only a region of especially efficient conduction, and, as far as we can tell, performs none of the peculiar brain functions.

The simplicity of this nervous system obviously harmonizes with the simplicity of the movements that the animal performs. We ourselves can make a thousand different movements at the bidding of our brains; the reader has only to think of all the possible ways in which his or her wrist and fingers can be moved. Now these hand movements involve the action of thirty-nine different muscles, and to each muscle there must run a separate bundle of nerve-fibres from the brain so that it may be properly controlled—thirty-nine separate and distinct nerve-paths from brain to hand! But for the one movement of the jelly-fish such an elaborate telephone system would be unnecessary. But

diffuse network suffices, spread over the whole bell and securing only that it beats together as a single unit.

The nervous system of a jelly-fish may be compared to a nightmare telephone system in which there is no proper exchange but only a tangle of wires; where the raising of one receiver would call up hundreds of subscribers, or indeed, if you spoke loud enough into it, every subscriber in the system.

The absence of definite nervous paths in the jelly-fish is easily demonstrated. It so happens that in many jelly-fishes (including the commonest kinds) the impulses for movement emanate from the marginal sense-organs. If these are cut off, the whole animal is motionless unless it be directly stimulated, by a touch for example, when it responds by a single contraction of the bell. But if only seven of the eight marginal organs are cut off, the remaining one suffices to keep the jelly-fish active; rhythmical impulses radiate out from it along the nerve-net to the muscles, and so the normal swimming movements are produced. Now in such a jelly-fish it is possible to cut the bell into any shape, into strips or spirals or other patterns, as Fig. 10 demonstrates, and in spite of such mutilations the contraction still spreads rhythmically from the marginal organ over the bell. So obviously there are no special conduction paths; the nerve-net conducts perfectly well in all directions.

The jelly-fish, then, presents an interesting stage in the growth of the apparatus of behaviour. It shows the three essential kinds of tissue. Some of its cells are specialized for the detection of stimuli (some for light, some for chemical substances, some for balance, and so on) and others are turned to muscle-fibres. Yet other cells, the nerve-cells, specialize in rapid conduction of messages from part to part. But this nervous system is astonishingly diffuse and decentralized, compared with our own.

In the evolutionary passage from cœlenterate to higher mammal, three important changes have taken place. The first is the supersession of a diffuse, directionless, all-per-

vading network of nerve-fibres by definite nerves, running, as telephone wires run, from one point to another without side-branches or wayside entanglements. As the range of possible sensations and movements is extended, these improvements in the telephone system become more and more necessary. The main steps in this transition still survive in the more primitive animals, where an extensive nerve-net is found side by side with a few special nerve-paths. Even in highly organized creatures the primitive network may persist in one or two parts of the body. The wave-

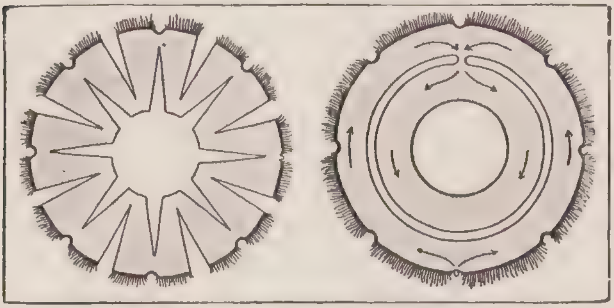


FIG. 10.—THE BELL OF THE JELLY-FISH AURELIA CAN BE CUT UP IN VARIOUS WAYS AND WILL STILL CONDUCT IMPULSES.

In these examples, pulsations spread rhythmically from the remaining marginal organ (see text) over the whole bell.

(*After Romanes.*)

like creeping movements of a snail's "foot" are controlled by a nerve-net, and so are the writhings of Everyman's intestine. But most of the nerve-fibres, in mollusc and man, lie in definite tracts or nerves.

As the telephone web of the body becomes organized in this way, a second parallel improvement is brought about in the speed with which nerve-fibres will carry their messages.

Here we have to break away for a moment from our telephone analogy. In a telephone wire the electric currents travel with an extreme velocity from mouthpiece to receiver.

But the "impulse" in a nerve is not an electric current; it is a change that runs along more like a ripple on the surface of a pond than an electric current in a wire. The first beginnings of nervous activity are by our standards impossibly slow. Even in surprisingly highly-organized creatures it may be hardly swifter. In the nerves of a fresh-water mussel, an impulse takes two or three seconds to travel an inch. In slugs it runs forty or fifty times as quickly. In king-crabs the messages from the brain to the muscles travel at about 10 feet per second; in a frog they do 70 or 80; in ourselves 400 feet per second—which is more than 250 miles per hour.

Perhaps the meaning of these facts will be most forcibly brought home by imagining a man with the nerves of a fresh-water mussel. Imagine that he carelessly let his cigarette slip between his fingers, so that it began to burn him. In something over two minutes he would feel the pain, and, if his brain reacted at once, the impulse to make him drop the cigarette would arrive at his fingers in another two minutes. But he would have suffered extensive organic damage in the interim.

Thus the telephone-cables of the body become more and more efficient as we ascend in the scale of Evolution. The third important advance is the development of a central exchange, the central nervous system, to which the nerves converge, where the information from the various sense-organs is received and collected, and whence harmonious impulses are sent to the various effectors. Only thus can behaviour be knitted together and the different parts be made to work as a single whole.

To go into the details of the nervous system in the various phyla of animals would take us deeper into biological technicality than we need to plunge. A few points of importance may be summarized very briefly.

In the echinoderms, such as sea-urchins and starfish, the nervous system is very much decentralized; the same may fairly be said of their behaviour. The main centre, a loop of

nervous tissue, runs round the mouth; from this five nerve-trunks depart, one along each of the rays of the body. But these five nerves are not simple telephone-cables, as our nerves are: they are governing exchanges like our spinal cords.

Each of the five arms of the starfish behaves with re-

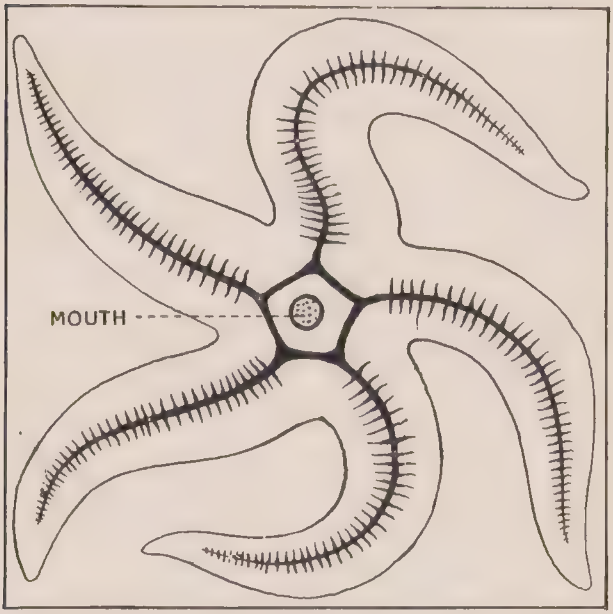


FIG. 11.—A DIAGRAM OF THE NERVOUS SYSTEM OF A STARFISH.
Five main nerves run along the arms from a central ring round the mouth.

markable independence; the creature is in many ways more like five individuals springing from a common centre than a single person with five fully subordinated limbs. A single arm, cut away from the rest, will crawl about on its tube-feet and turn over again if put the wrong way up. When a starfish is thrown on its back, each arm tries to right itself

by twisting over at the tip, gripping the ground and pulling. When one arm gets a secure hold it sends nervous messages to the others, which then stop their endeavours and stay passive, so that the first arm pulls the whole animal over on to its normally lower face. These nervous messages are sent by way of the ring round the mouth. If the ring be cut between each pair of arms, there is no co-ordination between them: if the animal is upside down, each arm goes on struggling to right itself, and, as they work against each other, the starfish simply ties itself into knots.

Moreover the starfish is covered with little stalked pincers, with which it defends itself against aggression and keeps itself clean. But these are best studied in its relatives, the sea-urchins, where they are larger and more numerous.

A sea-urchin is a hollow, bony ball bristling with spines. Each spine can be moved about; it has a ball-and-socket joint at its base, and a special set of muscles that move it. In among the roots of the spines is an undergrowth of the little stalked pincers. If an enemy approaches, the spines at that side of the sea-urchin turn like lances towards him, and the jaws below stand up, ready in case he should get to close quarters. Now none of these things are due to impulses from a central brain. Each spine, each stalked beak has a little reflex system of its own, and reacts independently of the others. Each is so constructed that it directs itself towards the chemical stimulus of an enemy. A tiny chip broken away from a living sea-urchin's shell, with only a single spine attached to it or a single stalked beak, will show the same alarm and preparation. Most of the behaviour of the creature is due to a similar summation of the automatic responses of its thousands of separately working parts. Any small animal touching the urchin is suddenly gripped by the tiny beaks, passed by the tube-feet and spines to the mouth and there eaten. Here, again, the parts are working separately. Von Uexküll, who worked on the behaviour of sea-urchins, speaks of them as "republics of reflexes."

But most animals are more centralized than this, and with the lower worms—flatworms, roundworms, bandworms and so on—the head comes into our story. Here for the first time we have animals which regularly progress with one end always in front; and as the head evolves with its special sense-organs and mouth, the brain appears and evolves with it. In these worms there is a simple brain in front, sending off two main trunks, one down each side of the body.

In annelid worms, such as earthworms and lugworms, and all the groups—crustaceans, spiders, centipedes and insects—which make up the Arthropods, there is a characteristic type of nervous system. The brain is in two parts, one just in front of the mouth and one just behind it; they are connected together by thick nerves, and the whole apparatus forms a dense ring round the animal's gullet. From this a single great trunk runs away, corresponding to our spinal cord, but lying along the belly instead of the back. In these creatures the body consists essentially of a chain of more or less similar segments, and in each segment the nerve-trunk swells out to form a little local brainlet, from which lesser nerves radiate out to the sense-organs, muscles and other tissues. The nerve-trunk of an earthworm may have over a hundred such subsidiary centres, one in each ring of its body.

That these swellings are indeed brain-like in their working was shown by some very suggestive experiments by Yerkes, subsequently confirmed by Heck. A narrow tube is made in the shape of a T, and earthworms are put into the stem of the T so that they creep along towards the cross-bar above. When they come to the parting of the ways, they can go either right or left. Should they go right, they get a gentle electric shock from a pair of electrodes concealed in the wall of the tube. Should they go left, they escape without this punishment.

Even a worm will learn. At first the choice of route is made at random, and the animal goes right as often as it

goes left. But, very slowly, the fact that the right-hand path is dangerous is forced upon its elementary intelligence. After a hundred trials or so, it goes left definitely more often than it goes right. After a hundred and fifty the lefts were found to outnumber the rights by about ten to one. Then

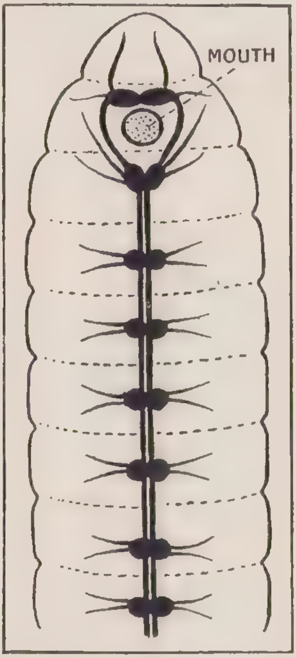


FIG. 12.—A DIAGRAM OF THE NERVOUS SYSTEM OF AN ANNELID WORM.

From a main nervous ring round the mouth, a double cord runs down the lower side of the body, with a swelling in each segment.

the electrodes were moved from the right-hand tube to the left-hand tube; slowly the worm unlearnt its first lesson and mastered the new one.

But the most interesting point is this. It was found that worms could learn in this way if the brain-mass round the

mouth was removed altogether; and even if, to make sure, the whole central nervous system of the first six segments was absent. So undoubtedly these swellings all along the worm's nerve-cord can perform a function which is confined to the brain in ourselves.

Sometimes this segmental arrangement may be modified.

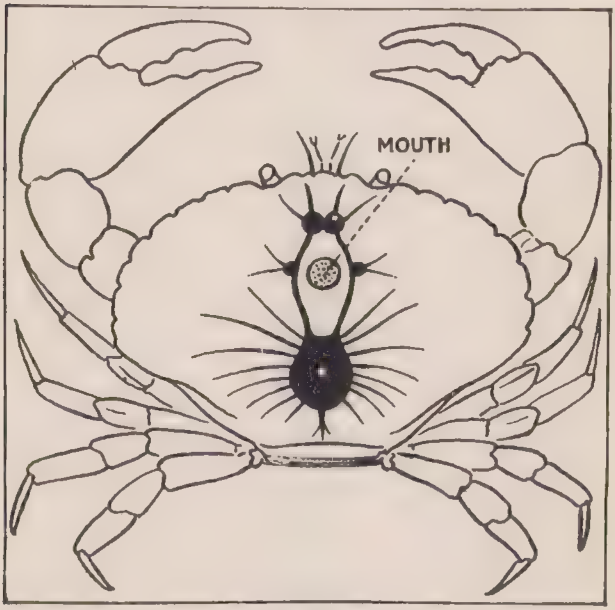


FIG. 13.—A DIAGRAM OF THE NERVOUS SYSTEM OF A CRAB.

It is built on a segmental plan (compare Fig. 12), but most of the "subsidiary brains" behind are gathered together into a single mass between the legs.

The most noteworthy alteration is the pulling together of a number of these subsidiary segmental brains into a single nervous mass. Thus the house-fly has, between its legs, what we may call a belly-brain, which seriously rivals its superior centre, the head-brain, in size. The same is true of crabs.

The state of affairs in snails, mussels and other molluscs is rather complicated. As in the arthropods and segmental worms, there is a ring of brain round the gullet which dominates the rest of the nervous system. From this ring two main pairs of nerves run off. One pair goes to a pair of subsidiary brains which co-ordinate the movements of that highly characteristic molluscan organ, the foot. The other pair goes to other subsidiary brains which supervise

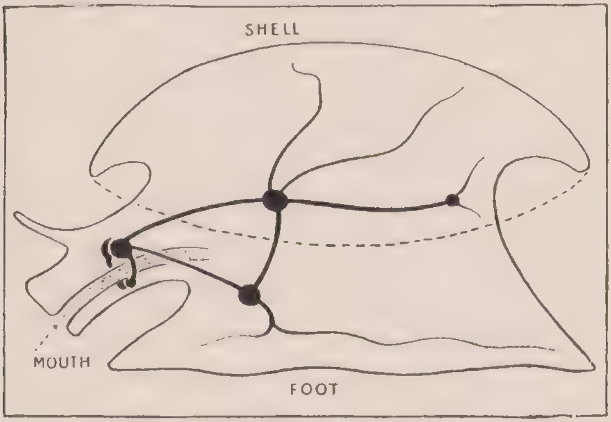


FIG. 14.—A DIAGRAM OF THE NERVOUS SYSTEM OF A MOLLUSC.

From a main ring round the mouth, cords run back to "subsidiary brains" controlling the viscera and foot.

the working of the digestive apparatus, gills and so forth. But into the details and variation that the group presents we need not penetrate.

Neither need we devote space in this section to the vertebrate nervous system. In the first Volume of this Series we considered it in detail in a single type, and we shall deal with its evolution more fully in a later chapter of the present volume.

§ 5

Vegetable Behaviour

The essential processes which underlie behaviour—nervous action, sensation, movement, and so forth—may be traced, as we have seen, in an elementary state in even the simplest animals, such as amœba. They take their roots from general properties of protoplasm. The body, as is well known, is a vast community of cells; any cell shows some measure at least of irritability, contractility and co-ordination. A dissociated cell creeping about in a tissue culture shows not only movement, but discriminative movement. Recently Dr. R. G. Canti has made a cinema film of such cells, speeded up so that their behaviour emerges very strikingly. One sees, for example, a cell creeping along; suddenly it is "attracted" by another cell, turns aside and moves towards it; crawls round it and over it. But the second cell apparently resents this close approach, for it struggles and moves rapidly away, leaving the first alone. With similar independence our white blood-cells consume bacteria and other things that have no business to be in our blood.

We have already stressed the difference between specialized and unspecialized cells. We can all add two and two together, or run fifty yards without excessive discomfort, or sing the first few notes of the National Anthem. An Einstein, a Nurmi, or a Chaliapine is simply a person who can do one of these things outstandingly well. Similarly a muscle-cell, a nerve-fibre or a sense-cell surpasses the general cell population of our bodies. But just as Chaliapine would lose most of his value were there no stages or opera-houses, or an Einstein if there were no books, publications and learned societies, so specialized cells require an appropriately organized body-community, whose elaboration increases with their specialization. When we turn from animal to plant behaviour we find the most remarkable

differences due to the different directions in which specialization has gone.

One often sees accounts in the newspapers of how in many ways plants parallel ourselves. They have beating hearts, we are told, and nerves like ours; they can be shown to tremble at an unpleasant stimulus, or to squirm in a death agony. Generally these accounts centre on a series of ingenious experiments conducted by Sir J. C. Bose, of Calcutta. Now, since contractility, conduction, and sensibility are general protoplasmic properties, one would expect to find something of the sort in plants. Irritability to different kinds of stimuli exists undoubtedly in plants, and in one or two cases a kind of slow transmission of impulses has been demonstrated which seems to parallel the "neuroid" transmission of an amœba or a sponge. Moreover, many plants, as is well known, exhibit various movements: opening and closing of flowers, turning of leaves towards the light, and so forth. These are, however, due in most cases to a rather different kind of mechanism from the contractile tissues of animals. The plant-effector is usually a pack of cells that can swell and stiffen by absorbing water and becoming turgid.

Here, then, plant behaviour parallels our own, but no more than does the behaviour of an amœba or a sponge. It is ridiculous to overstress the analogy; to speak, for example, of a plant having nerves like ours simply because it shows crude nerve-like transmission. In another instance Bose has detected rhythmical pulsations in the central tissue of stems, and interprets them as the motive-force that drives sap upwards. They may be—although it has been denied by several botanists—but it is certainly misleading to speak of such pulsations as heart-beats. The writhings of Everyman's bowels are a hundred times more closely akin to the beating of his heart than are these alleged pulsations in plants.

Evolution is commonly presented as a process leading up to and culminating in the crowning human brain; but

let us remember that while this slow growth was in progress another evolution was going on, starting from the same microscopic origins, but taking an altogether different direction. The plant design began with a green scum of microscopic life-specks; it elaborated and perfected itself through alga and moss, through fern and horse-tail, to the grasses, flowers, and spreading trees of to-day. Gradually the stem stiffened and straightened, the roots and leaves and pipes for fluid transport became more intricate in design and efficient in functioning, and strange ways of securing fertilization and distribution came into being. Yet all the time the vegetable stock was minimizing the nervous and muscular phenomena that we prize so highly. The rudimentary powers of sensation, conduction and response, latent in its protoplasm, remained unexploited. Plants are green; they have no need to hunt or forage; so the vegetable stock evolved upon fundamentally different lines.

The main activity of a plant is not discriminating movement, but discriminating growth. It spreads its leaves towards the sun and its roots down into the soil. In this it shows a certain parallelism with our own behaviour; for it grows in this direction and avoids that much as an animal moves in this direction and avoids that. Anyone who sees a speeded-up film of plant behaviour will at once recognize this parallelism.

Take a particular case: the growing root of a nasturtium seedling is photographed every fifteen minutes. The resulting film is run through the projector at the ordinary rate of fifteen pictures a second. The rate of movement has thus been magnified 13,500 times, and the behaviour of the root-tip now seems that of an animal instead of a plant. It pushes its way like a white worm through the soil; like a worm's head, its advancing end waves from side to side as it moves onwards; like a worm, it avoids obstacles by bending and crawling round them.

The same apparent acquisition of the attributes of an animal as a result of mere change in the tempo of behaviour

is seen in nearly all such speeded films. The nasturtium bud, which takes all a morning in its slow expansion into a flower, becomes alarming like a lion suddenly throwing open great jaws; the snowdrop folding its petals and drooping its blossom during the hour before sunset, has the air of a man relaxing his limbs and hanging his head on his breast in sudden grief. The horse-chestnut twig, emerging so slowly from its winter dormancy that its movements, its onward growth, its putting forth of successive leaves one by one, its alternate slow rotation, a little to one side and then to the other, are as imperceptible as those of the hour hand of a watch, suddenly acquires all the life and grace of a dancer.

This appearance is not deceptive. The reactions of plants are indeed not dissimilar to those of many lower animals; and the fundamental difference is precisely a difference of rate. The plant, rooted in the soil, cannot escape danger by flight, or capture food by active pursuit; rapid reactions are therefore, with rare exceptions, pointless, and its movements are almost wholly self-centred, devoted to attaining the right position for itself and its organs, unrelated to enemies or to prey or to any rapidly moving object whatever. That being so, they can be executed quite well through the slow agency of growth, and no special rapid machinery such as muscle has ever been needed or called into existence.

Two main outside forces influence the direction of plant growth. The first is gravity; leaf-bearing stems tend to grow upwards (as is very easily shown by growing seedlings in the dark), while roots tend to grow downwards. The second is light; stems grow towards light, and roots (for instance, in a seedling suspended in the air and illuminated from one side) grow away from it. A third factor, moisture, may also play a part; in most cases roots grow towards moist regions in the soil. Responses of this kind are called *tropisms*; and, as we shall very shortly see, the word has a similar application in animals. The response to light is

called *phototropism*, that to gravity *geotropism*, and that to water *hydrotropism*. As a further verbal complication, if the plant grows towards the stimulating influence its tropism is called positive, while if it grows away it is called negative. Thus a leaf-bearing shoot is positively phototropic and negatively geotropic ; while a root is negatively phototropic, positively geotropic, and positively hydrotropic. The utility of these phrases will soon become apparent.

§ 6

Instinctive and Intelligent Behaviour

While plants specialized in directional growth, animals took the other road and developed an apparatus for directional movement, with the more refined sensitive structures that this faster method of response necessitates. But for all their muscles, sense-organs, and brains, animals may be ruled in their activities by external influences as slavishly as plants are.

While these lines are being written, a little zoo of insects is flying in, one by one, through the open window from the night outside. As they enter, the pilgrims go straight for the object which has fascinated them and drawn them in—the acetylene lamp on the table. They flutter round it and crawl over the shade ; some are held by the white circle of light it throws on to the ceiling. Sometimes one of them finds the way round under the lamp-shade and flies straight for the hypnotizing glare—only to fall, burnt or dead, a second later. One fat moth fell with a flop at the heat, then pulled himself together, rose and, undaunted by his experience, made straight for the white glare again.

Sir E. Ray Lankester wrote of a house in Java in which an open lamp was lit every night.

> Regularly two sets of animals . . . arrived on the scene. Swarms of moths and flies dashed in and out of the flame and fell, maimed by

the heat, to the ground. There a strange group had already assembled. Gigantic toads and wall-lizards crept from their holes in the masonry and woodwork and awaited the shower of injured insects, which they snapped up in eager rivalry, as the infatuated flame-seekers dropped, hour after hour, to the floor. (*Diversions of a Naturalist.*)

A kindred case was observed by Loeb. If you take a number of prawns and put them in a dish through which a gentle electric current is continuously passing, they will show no sign at first of awareness of the current. But in a little time every one of them will be at the end of the dish which is connected with the positive pole of the battery. The prawns seek the anode as slavishly as the moth seeks the lamp. Various other creatures can be similarly influenced by a weak electric current. The slipper animalcule, for example, always swims to the negative pole—the opposite direction to the prawn.

How are we to interpret these facts? In these last-mentioned cases, obviously, the bias is of no value to its possessor, because weak electric currents of this kind never occur in nature. It is a purely accidental phenomenon. In the case of the prawn the nerve-fibres in the central nervous system lie in different directions, according to the muscles with which they are connected; and it is known that a constant electric current will affect the activity of a nerve-fibre according to the angle at which it happens to cross it. In a prawn which happens to be facing the positive pole, the nerves to the muscle which push it forwards are made more active, while those which carry it backwards are enfeebled. In a prawn facing the other way the reverse occurs. So that the first prawn progresses somewhat more vigorously and easily than usual, while the second goes with labour and difficulty, until it happens to turn round. It is as if they were living on the side of an invisible hill. Just as in the latter case gravity would be constantly urging them down the slope, so the current constantly urges them to the positive end of the tank.

Something of the same kind happens in the case of the

insects that fly into the light. They are so made that the angle and intensity of the light that falls into their eyes affects their muscles viâ their nervous system; and they tend to fly towards the light as infallibly as a prawn tends to make its way towards the plus end of its electrified aquarium.

Gravity can act upon animals in a similar way; there are earth-seekers which tend always to direct their course downwards, and earth-shunners which tend to travel upwards.

The parallelism between these slavish responses to physical factors and the tropisms of plants, which we described at the end of the last section, was first stressed by Loeb. He extended the words phototropism, geotropism, and so forth, to animals. Movement directed by an electric current is called galvanotropism. Moreover, Loeb performed a number of pretty experiments to show the automatic, mathematical way in which the animals were driven by their inner urges.

For instance, he tried the behaviour of phototropic animals in the presence of two lights. If both were equally bright, the animals generally went, not to either light, but in a direction that led half-way between them. This shows that they seek the light because of a simple automaticity and not because they like light and deliberately seek it out, for in the latter case they would go to one light or the other. If one light was stronger than the other, the animals took a course with a slight bias that way, and its angle could be calculated very accurately by means of a simple mathematical formula. In another series of experiments rapidly flashing lights were used, and here it was found that the pull a light exerted on the creature depended on a straightforward relationship—it was proportional to the product of the light's intensity and its duration—which is parallel to what we find in certain simple light-produced chemical reactions, like the changes that occur in a photographic plate during its exposure.

These experiments were, of course, prepared under simpli-

fied conditions; in nature the action of a tropism is often counteracted and delayed by a host of other stimuli and reactions. The insects that make for the light do not go altogether blindly and directly; they may pause on the way to chase or avoid each other, or to rest for a little while. But sooner or later they get there, just as a feather floating in the air will sooner or later come to earth, though on the way it may indulge in all sorts of devious twists and flutters. Under natural conditions a tropism is a sort of directional urge that runs through the behaviour of a creature, and gives it a pervading bias, perhaps conspicuous, perhaps hardly noticeable, but always in a given direction.

Galvanotropism, we noted, is useless to its possessors; the positive phototropism of a night-flying insect is not only useless but sometimes, in the neighbourhood of human habitations, definitely destructive. But often a tropism plays an important adaptive part in the life of a creature. Some animals, like the roots of a plant, are negatively phototropic; a blow-fly grub will crawl away from the light in a straight line, and, as it lives buried in decaying things, the helpfulness of this tropism is manifest.

Moreover, in many cases the sense of a tropism can be reversed by other conditions. Thus barnacle larvæ seek light in the cold and avoid it in warmth; similarly many small aquatic crustaceans, such as the water-flea Daphnia, tend to swim downwards in a bright light and upwards in darkness.

There is a very pretty case in which such a change of tropism underlies a complicated instinct. The caterpillars of the goldtail moth *Porthesia chrysorrhæa* hatch in autumn and spend the winter hibernating in nests near the ground on the stems of the shrubs on which they feed. In early spring they leave the nest and crawl straight up the shrub to the tops of its shoots, where they find the first buds beginning to open, and these they devour. The coming out from the nest is apparently a response to warmth, for they can be made to leave it at any time in winter by warming

it artificially. But why do they crawl upwards—how do they know that the only place where they can find food is at the tops of the branches? If they went downwards they would starve.

They do not know. This upward creeping can be shown to be a simple positive phototropism, directed by the light reflected from the sky. If some of the caterpillars are taken as they are leaving the nest, and put in a glass tube lying near a window, they will all collect at the end of the tube nearest the light, and stay there. If the tube is turned round they will crawl to the other end, again towards the light, and there wait. Most surprising of all, if a few young leaves from their food-shrub are put at the other end of the tube, the end farthest from the light, they make no attempt to reach the meal; the light-rays hold them captive at the end nearest the window, and here they stay until they starve.

Under natural conditions the tropism guides them up to the only place where they can find their food. But there is a further complication here. For only an unfed caterpillar is positively phototropic; in some way nourishment removes the tropism, and after eating light has no effect. The utility of this is clear. The caterpillar quickly clears up the leaves at the top of the twig, and if its slavery to light persisted it would have to stay there and starve. But having eaten it is freed and can creep in any direction; the experiment with the glass tube and the window now has no result. So it is able to work its way downwards and find the lower buds as they begin to open.

A tropism, then, is a blind and unreasoning drive within an organism, it may lead the creature to destruction or to salvation, but in either case it is a simple result of the interaction between the inborn structure of the nervous system and stimuli from the environment.

Another kind of response, equally blind and unreasoning, is the reflex. As an example of a reflex we may take the automatic movements of the hand when the fingers touch the red end of a cigarette. We shall note many other

examples in later chapters. The differences between a reflex and a tropism are two. Firstly, a reflex usually only concerns a part of the body (in this case, the hand), while a tropism affects the position and movement of the body as a whole. Secondly, in a reflex an abrupt reaction is elicited by some sudden change in the environment, while a tropism is more a steady, underlying bias in behaviour, brought about by a constant stimulus. But the distinction between the two will become clearer in later sections, as we handle the words.

Between them, tropisms and reflexes underlie most of the phenomena usually loosely called "instinct." The flying of the moth into the flame is often spoken of as an injurious instinct. Young chickens when they hatch have the instinct to peck at any small object that they notice lying on the ground; but soon experience teaches them to distinguish the edible from the inedible. In this case the first instinct is a reflex.

Instinct is rather a dangerous word, because it has been used in a variety of senses in ordinary speech; any unconscious impulse may find itself labelled instinctive. But here we are going to restrict the term to those elements in behaviour which are inborn in the organism, or which develop in later life (as the beard and deep voice of a human male develop) as a simple result of the organism's own constitution. Instinct is congenital behaviour. Contrasted with instinct we have all those elements which depend upon individual experience—upon memory and learning. These, for want of a better word, we may call intelligent behaviour.

Every animal comes into the world with a certain inherited endowment of congenital behaviour. Some go through life with that alone. Before we carry our analysis any further, it will be well to consider an example of that kind. But most animals learn as they live; as we ascend the animal scale we find them extending and improving on their original outfit, sometimes only slightly and sometimes very considerably, by personal adaptability and experience.

Finally, in ourselves intelligent behaviour outweighs and largely supersedes instinct. Our next chapters will trace the interrelations of the two kinds of behaviour, first in the highest and most interesting invertebrates, and then in the group to which we ourselves belong.

But first we must introduce ourselves, by means of a microscope, to a creature whose behaviour is entirely congenital.

§ 7

The Behaviour of the Slipper Animalcule

If we take a few bits of water-weed from a pool in summer —preferably a stagnant pool—and leave them in a glass of rainwater to rot, in a few days we shall very probably see a multitude of white specks in the glass, on holding it up to the light. These specks, the largest ones about a third of a millimetre long (an eightieth part of an inch), are slipper animalcules. The rotting weeds have first nourished a host of bacteria, visible perhaps as a faint turbidity in the water, and the slipper animalcules, tiny but ravenous beasts of prey, are now living on their very much smaller neighbours.

The appearance of a slipper animalcule (Paramecium is its technical name), when magnified with a low power of the microscope, is shown in Fig. 15. It is covered with cilia—the minute, vibrating, hair-like projections that we also possess in the lining of our windpipes—and by means of their almost ceaseless lashing it swims rapidly along. But the cilia are not all alike; some are stronger than others and the direction of their lashing is not quite the same as the long axis of the body. Because of these facts, and also of a curious twist in the front end of the creature (its body has been likened to a leaden rifle-bullet twisted by being shot through a grooved barrel), it swims in a spiral course, spinning round and round on its own axis as it travels forward.

About half-way along the body is a wide funnel-shaped

pit, which sinks in towards the middle of the body. This is the mouth; like the rest of the body surface it is covered with cilia, and their lashing keeps a whirl of water flowing into the funnel, where such nourishing particles as bacteria are seized and swallowed.

Paramecium is one of the biggest of the better-known protozoa, and, as with the rest of the group, it has an organization like that of a single cell from our bodies. Most of its interior consists of viscid fluid protoplasm; in the centre somewhere is a large nucleus with a smaller one (or perhaps two) lying beside it. Any food particles that are taken in at the mouth pass into the interior contained in little water-

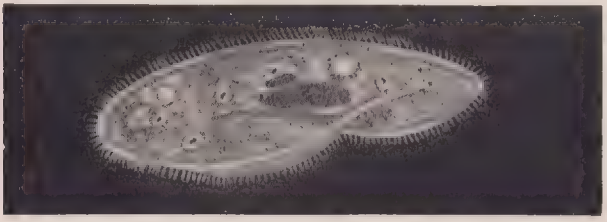


FIG. 15.—*PARAMECIUM CAUDATUM*, THE SLIPPER ANIMALCULE.
(*Photo by H. Bastin.*)

filled cavities and thus drift round the body, being slowly digested.

By our standards, the ways of a slipper animalcule are as strange as its structure. It multiplies by tearing into halves after the manner of protozoa, and it is neither male nor female, for its equivalent of the sexual process, divorced from the reproductive function, is an affair between exactly similar individuals. But here we are not concerned with these rarer adventures; it is on the humdrum daily business of feeding and self-preservation that we shall concentrate our attention.

As we watch a paramecium bustling its spiral way across the field of the microscope, we may chance to see it give a highly characteristic and important reaction. Suddenly

it stops, darts swiftly backwards, turns slightly, and then starts swimming forward again in a new direction. This is called the "avoiding reaction"—we have met with it earlier in this chapter (p. 8) in that other ciliate Stentor—and it means that the animalcule has come up against something that it doesn't like.

Suppose that some kind of obstacle, such as a bit of plant debris, blocks its path. As soon as it touches the barrier the creature gives this avoiding reaction—starting back, turning, and trying a new line. Perhaps this still does not clear the obstacle; if not, there is another collision and another avoiding reaction, and so on until the paramecium gets round. There is no system in this exploration. It is a perfectly random affair; the animalcule turns first in one direction and then another until it happens to get clear.

Exactly the same reaction is given if very strong light suddenly falls on the animal, or if it gets into water which is unsuitable—too hot, too cold, too salty, too acid, or too alkaline. To all these unpleasant stimuli paramecium has but one answer; and it repeats this answer until it either perishes or else escapes into better conditions.

The details of the avoiding reaction may vary according to the nature of the influence that calls it forth. Sometimes the backwards movement is considerable while at others it is slight; sometimes the change of direction is greater than at others; and so on.

This "try, try, try again" of a single form of response we may call the Method of Trial and Error. In paramecium, we see it in its simplest form. But it continues to be employed in one way or another on every level of behaviour up to the human. A dog with a stick in its mouth is trying to get through a set of railings; it turns its head now at one angle, now at another, it shifts the stick in its teeth, it tries over and over again without any evident system in its investigation, until finally one position allows it to pass—that too is trial and error. So, too, on a more elaborate level, is the behaviour of a man seeking frantically

to escape from a room in which he has been locked, as he rushes round and hammers the walls, in the hope that by chance he will hit on a weak spot. So, on a different level once more, is the behaviour of the scientist when confronted with a strange fact to whose solution his previous experience suggests no obvious line of approach, he tries what Darwin called " fool's experiments " in the hope that one or other of them may yield a clue. But as we go up the scale, the method of trial and error ceases to dominate behaviour, it becomes a tool in the hands of this or that instinct or desire, as when the dog with the stick desires to get to his master through the railings ; it becomes modified by experience and intelligence, as in a prisoner trying to break out of his confinement and examining his cell systematically ; and, finally, in man it becomes supplanted, to a certain variable extent, by deliberate planning. But the idea of " have a shot at it " is always there, from Paramecium to Plato, and if it was indispensable as the master of the protozoan activities, it remains equally indispensable as the exploratory scout of man.

As Jennings (an American investigator) showed, almost all the apparently purposive behaviour of paramecium depends solely on the repetition of this piece of automatism. Normally the stagnant waters, full of decaying vegetation, which it inhabits, are slightly alkaline. Where, however, a multitude of the bacteria on which it chiefly feeds are collected, the carbon dioxide they give off will make the water more acid. It is, therefore, an advantage for paramecium to find and stay in any region of slight acidity. That it does so can be easily demonstrated. If a number of paramecium be put in a drop of water between two slips of glass, and then, by means of a fine pipette, a bubble of air and a bubble of carbon dioxide be separately introduced into the tiny aquarium, the carbon dioxide bubble will soon be surrounded by a dense ring of animalcules, while the air bubble will be neglected.

As more carbon dioxide passes into the water, the ring

of paramecium will move slowly out from the bubble, the water immediately against it being now too acid for comfort. If, during this latter phase, we watch our little experimental world through a low-power microscope, what we see is this: if a paramecium happens to swim from the general drop into the region of the crowded ring, it gives no reaction, but swims on with its normal spiral. When it reaches the region of the stronger acid on the inside of the ring, however, it gives an avoiding reaction, and changes direction; and it does the same if now, swimming back again, it reaches the neutral water on the outside of the ring. So it continues, giving the avoiding reaction every time it gets to the edge of the ring, and the acidity becomes too high or too low. Thus by means of its sensitiveness to high or low acidity, and its single answer to both, the paramecium becomes trapped, but trapped in the middle zone where the conditions are best (Fig. 16).

Precisely similar behaviour can be seen when drops of weak acid or of various salt solutions are used; in each case the animalcules wander by chance into the most suitable regions, but, once there, refuse to leave them; and we have the paradox that paramecium is guided in its positive behaviour by a negative reaction.

The creature does, however, exhibit a positive piece of behaviour which is directly advantageous to it. Its bacterial prey has a habit of swarming together and forming raft-like collections of great numbers of individuals. If a paramecium is guided to the faintly acid zone round such a raft by its avoiding reaction, it will obviously be advantageous for the animal to stop swimming and anchor itself directly to the bacterial raft. This is done by means of a characteristic reaction to solids. Whereas strong mechanical contact (such as is produced by the creature suddenly bumping its front end against a hard obstacle) calls forth the avoiding reaction, light touches, especially with objects of irregular and thready surface such as the bacterial raft or a scrap of paper, bring about a total stoppage of the cilia on

the side touching the object. The other cilia also slow down, except for the ones round the mouth, which continue actively sucking food towards the mouth. The result is that the paramecium stops and browses over the surface it has discovered. It is interesting to note that when the animal is doing this its sensitivity to other agencies is diminished—its attention, so to speak, is occupied by its meal—a

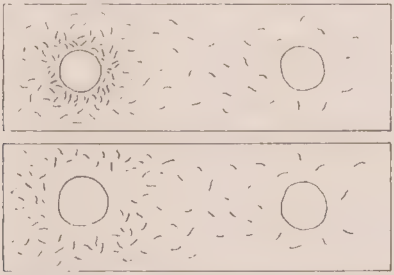


Fig. 16.—A Number of Slipper Animalcules, imprisoned between two slips of Glass, show their liking for faintly Acid Regions.

Above, they collect round a bubble of carbon dioxide (left), which dissolves in the water, forming an acid, and neglect a bubble of air (right). Below, some time later, the water round the carbon dioxide has become too acid for comfort, and the creatures now lie in a ring where the acidity suits them better.

phenomenon which is of course paralleled in our own behaviour.

This second reaction, in spite of its simplicity, is obviously of service to paramecium under natural conditions. The rough, solid objects which elicit it will, in general, be rich in nutritious particles. But the experimenter can show how mechanical and unreasoning a thing it is; Jennings found that paramecium would stop and browse eagerly but emptily over such objects as scraps of paper, fine fabrics, threads, or heaps of carmine powder, in spite of the fact that "the cupboard was bare."

In addition to these two reactions, paramecium may respond by a directional bias in its swimming to one or two

simple physical agencies. For example, it is negatively geotropic; it tends to swim upwards, against gravity. In the pools it inhabits it does not feed on the bottom but swims about in the upper layers of water, finding out and browsing over floating particles in the manner we have described. The sense-organ by which it feels its way upwards is, apparently, its digestive apparatus. Paramecium has of course no permanently marked-off alimentary tube, but when it eats food-particles it takes them into little vesicles of water, in which they drift round its body. Each of these little vesicles, or "food-vacuoles," is in effect a stomach and intestine combined. Digestive ferments ooze into them from the living protoplasm around; the products of digestion are absorbed out of them. Now the food is in general heavier than water, and so it comes about that the food-particles rest on the lower sides of these temporary stomachs in which they are enclosed. It would seem that the paramecium can feel this, much as we might feel a small but heavy object in our stomachs pressing downwards, and that this is the only way in which it gets any sense at all of up and down. If the reader can stretch his imagination sufficiently, let him be mentally floating in water (not on it), with eyes closed, with the balancing organs in the ear temporarily paralysed, and only the pressure of a small hard object in the stomach to tell him which way up he is. It is possible to trick paramecium because of this fact. By inducing it to swallow grains of finely powdered iron or nickel and then holding a powerful magnet over it, the animal can be persuaded that up is down, and its reactions can be reversed accordingly.

But this response to gravity only takes place if the water is faintly acid. In neutral water there is no reaction. Apparently it depends for its manifestation upon the physiological state of the animalcule. This typifies a set of phenomena of very great importance; a number of reactions which occur with machine-like regularity in one set of conditions are changed or fail to appear altogether when the

conditions are altered. We met a similar case in the caterpillars of *Porthesia chrysorrhœa.* A great deal, perhaps all, of the variability and apparent spontaneity of the behaviour of lower organisms is due to such alterations of physiological state ; and we have only to think of our own feelings and reactions to food when hungry, just after a good meal, and when on the verge of sea-sickness, to realize that in higher forms also they play a leading part.

Thus, by means of a few simple and perfectly automatic reactions, the slipper animalcule swims about, seeks and consumes its prey, and avoids hostile influences. To us it is almost incredible that so small an equipment should suffice. If an anima like a pig, say, or a deer were to live with such slender resources, it would normally bustle along, bumping into trees and rocks, and only able to get round obstacles by backing away for a few steps, turning into a new direction at random, and starting off again. Put in a small pen with an open gate, it might give ten or twenty such reactions before it hit the way out. When it smelt a suspicious smell, it could not make off in the opposite direction, or wait warily and find out just what kind of potential enemy was the cause of the smell, or what it was doing. It could not see or snuff its food from afar, much less learn its way about its locality and remember where to find the best grass and juiciest thickets, but would be reduced to careering along, brought to a standstill now and again by the feel of herbage or leaves on its legs ; and indeed, it would not seek for its food at all, but would simply happen upon it by luck. But for paramecium, swimming about in a bacterial soup, such reactions are enough, and thus these tiny, single-celled creatures conduct their lives.

Can we imagine so limited a creature as having a conscious mind ? Let us assume so for a moment, and see what kind of mind it must be if it exists at all.

The first important difference between its experience and ours is that it has no special sensory apparatus, such as the eye or the ear, for determining the direction from which

such agencies as light arrive, nor for determining their relation to each other in space. It knows nothing but its own body, and the things that touch its body. Neither has it, as far as we can judge, much power of discriminating between different kinds of influence; it gives one reaction only, the avoiding reaction, to such diverse conditions as a hard obstacle, too-acid water, too-alkaline water, salt water, hot water, chilly water, and so forth. Presumably it experiences but one kind of sensation for all these things, since it gives but a single response. So that we can read into the mind of our paramecium no variety of qualities, colours and tones; no images, no sense of near and far; at most, nothing more than monotony of faint pleasure and displeasure.

Secondly, paramecium has no memory. It gives no sign of profiting by experience; even the dodging by which it tries to get round an obstacle is random and unsystematic. Sometimes indeed it shows quite transitory changes of intensity or kind of reaction, after long repetition of the same external influence, but these are merely fatigue effects and not expressions of a memory faculty at all. It reacts differently because it is tired. Paramecium's life is forgotten as soon as experienced. The animal recalls no past and anticipates no future, but lives life after life, as it were, in a perpetual chain of "nows."

Specialists in the study of protozoa rank paramecium as a highly-organized member of the group. One could find even simpler lives. Amœba, for instance, does not swim by rippling cilia, but oozes along by a kind of viscous flowing of its whole body. It lacks a special mouth, and embraces and takes in its food at any point on its surface. Its behaviour is as simple as or simpler than that of the slipper animalcule. Going lower down the living scale, we find kinds of bacteria which do not move at all; which do not eat, but simply absorb their food; whose only activities are growth, sexless reproduction, and the automatic exudation of various chemical materials. We find the life, like the

structure, is at or below the cellular grade; there is as much behaviour—sensibility and activity—in one of our Everyman's white blood-cells, or in a connective-tissue cell in a tissue-culture, as there is in these elementary free-living creatures.

§ 8

The Different Worlds in which Animals Live

There are two great mistakes into which everyone, it would appear, falls by some kind of inevitable tropism when beginning to observe and think over animal behaviour, and it may be well before we go further to devote a brief section to their discussion. One is to ascribe to animals the higher faculties of human mind, such as intelligence, purpose, elaborate emotional states like hopes or fears or aspirations, powers of rapid learning, of imitation, of recalling an idea. The other is the assumption that the world in which animals live is that world of objects and events in space-time in which we pass our lives. The ascription of human faculties to animals underlies all the familiar stories of dog intelligence, all the pleasant anecdotes of dozens of books on popular natural history. We shall have occasion to prick that bubble, regretfully but decisively, in several of the later sections of this volume. But this is perhaps the place to discuss our other point.

When we say that the world of a beetle is different from that of a dog, and both from that of a man, we naturally do not mean that the external reality in which a dog lives its life differs from that in which a beetle lives. But the nature of external reality—that is a problem for the philosophers. What concerns us as biologists is the nature of the external world as it touches and appears to the animals, the world as it effectively is for them. The world of a slipper animalcule does not consist of a number of objects as it does for us, each object, like a tree or a dog, possessing a number of properties, some concerned with shape, others with

hardness and heaviness, others with temperature or smell or taste or colour. There are no *things* in its experience, only separate stimuli; it apparently has no capacity for perceiving two kinds of stimuli joined up into one compound experience, for thinking them together, as we do when we think of the yellowness and roundness of an orange. There is no space in its experience, no right nor left; it has no capacity for telling where anything is in relation to anything else; nor can anything it experiences have a shape—all the stimuli that beat upon it are as formless as smells are to us. And there is no time in its experience; it lives only in the narrow boundary between the past and the future. Once an experience is past, it is blotted out for ever; past and future have no meaning and, indeed, no existence for paramecium.

Most of the lower animals live their dim and windowless existence in a world of this limited kind. Let us think of one or two.

A jelly-fish bell is an arrangement of nerves and muscles which has only one answer to all the possible questions which our varied universe can put to it: it can pulse. It can vary the emphasis of its answer by pulsing more strongly or less strongly; that is all.

A sea-urchin is a feudal system of reactions, but a feudal system without a king. The barons occasionally combine, though they enjoy a great deal of local independence; but there is no brain-parliament where the local lords can pool their ideas. There is in the sea-urchin almost no apparatus for putting together the experiences of the parts and making a single experience for the sea-urchin as a whole.

The worm, the mollusc, and still more the arthropod, have the makings of such an apparatus: yet their sense-organs and their brains often do not permit their experience to be anything very elaborate. Even for such a complicated creature as a snail, for instance, the sun does not exist; there are only degrees of light and warmth. Its only adumbration of the existence of objects is that there is light here and dark there, in ill-defined patches. And it cannot see

things. It usually becomes visually aware of objects when they are between it and the light; and then they are merely shadows of more or less intensity. The world of crustacea begins to acquire more of a framework and a greater richness within the framework. A crab scuttling over the shore at low tide can see on which side of him you are approaching; and objects begin to exist for him, because he can distinguish something of sizes and of flat shapes, if not of solidity. But, all the same, the shapes are wretchedly blurred and dim; he sees men as trees, walking; his visual world is little but a world of dark dangers of different extent, between which he can draw no further distinctions.

To such creatures as hermit-crabs, objects with solid shapes begin to exist. This is more or less of a necessity for them with their shell-inhabiting propensities; and experiment has shown that they can distinguish spheres from cubes and flat from pointed cones.

With the perfection of the eye as an image-forming camera instead of a mere light-perceiving organ, and with brains capable of linking up impressions from other senses like touch or smell with those from sight, the world of evolving life grows rapidly richer; it comes to have some resemblance to the world we know, by consisting of solid objects in space. When a bee is flying to and from its hive, across our garden, it sees the same objects as we do. It may not know that this is a chair or that a tree; but at least it sees them and distinguishes them.

Even so, the world of such a creature may differ from ours in many ways. It may, for instance, be a world of black and white, since the animal has no colour-sense; this is not true of bees, but even dogs and cats can see only in black-and-white. Or again most insects are deaf, so their world is soundless.

There are other frameworks in our human world besides that of space; there is the framework of time and the framework of cause and effect. These evolve long after that of space. The story of the evolution of mammalian intelli-

gence, which we shall give in a later section, is in large part a story of life making groping experiments in the direction of these new frameworks. A dog is just beginning to put two and two together; but his powers in that direction bear about the same relation to our human capacity for digging out causes and drawing deductions as the power of a crab's eye to distinguish the shape and pattern of things does to a dragon-fly's or a bird's. So with time; the non-human animal does not have its life fitted to a framework of time. The past may be alive in the present for it; but so far as we know, the past does not exist in its own right, as it does for us, as something to which we can have access when we wish. The length of time for which an animal can hold an image in its head is very short; the image speedily gets crowded out by the insistent throng of new sense-impressions. It is probable that no animals below apes can call up images of past events as we can; a dog probably is incapable of remembering and reflecting about his absent master, although he recognizes him again at once on his return, even after years. This lack of imagery and recall too makes the animal's time-framework a poor one.

With man and man's greatest invention, language, the world once more becomes richer: it becomes an orderly whole with at least the possibility of having all its aspects related one to the other.

Cell-colonies acquire a purely physical unity; they are marked off in space; cell-colonies then become many-celled animals, and the nervous system confers on them a unity of behaviour—they act as wholes; the human cerebral cortex provides men with an inner unity of experience—their world of thought becomes a single whole. Looked at from a slightly different angle, we see the aggregates of cells we call higher animals acquiring a physical unity quite early in their evolution; but only at the very end, in man, do they come to possess an individuality of the inner conscious life. Before, any inner life there may have existed

has been a mere aggregate of shreds and incidents of consciousness; now it becomes organized—a personality.

There are thus three main kinds of worlds in which animals live. There are spaceless, timeless worlds consisting of mere stimuli. There are worlds consisting of stimuli put together to make objects, things with shapes and sizes. And there are worlds of space and time, of objects held together in bonds of cause and effect to make orderly constructions.

These are the three main stages in the evolution of the world as it is known to life. They are connected by every possible transition, and the evolution is still proceeding. Our sun is a very different sun from Abraham's; it is much bigger, much farther away, and much hotter. Even our framework of space has recently changed.

We are often apt to think that our capacity for changing our thought-constructions—as when we abandon the flat earth for the round, the central for the merely planetary globe, the first chapter of Genesis for Evolution—is something specifically human. So in a sense it is; for it is only we men who have got any such elaborate thought-constructions to change. But it is also the culmination of the same slow process which was begun when life first began to enlarge its world by increasing the range and number of the bare stimuli to which it could respond.

CHAPTER II

HOW INSECTS AND OTHER INVERTEBRATES BEHAVE

§ 1

The Arthropod Mind as the Culmination of Instinct

TWO only of the various streams of evolving animal life have attained outstanding success. These are the vertebrates and the arthropods. In earlier Volumes of this Series we stressed the radical differences between their two plans of construction, and we pointed out some of the differences in their evolutionary fate. We shall here discover an equally profound divergence between them in behaviour and in plan of mind.

The mammals, with man at their head, and the insects, with ants, bees, and termites as their highest specialization, are the culminating branches of these two divergent stocks. The divergence began with obscure details of bodily chemistry and construction, such as the preference of insect tissues for secreting chitin, and using it for a skeleton on the outside of their bodies, of vertebrate tissues for making cartilage and bone and using it as an internal scaffolding. The vertebrates went in for tails and for limbs restricted to two pairs, the arthropods for taillessness and a whole battery of appendages.

There were many other differences, but we need only stress the fact that land-vertebrates breathe by lungs, land-arthropods by air-tubes. This fact is not so unconnected with our present subject as it seems, for it was air-tube breathing which limited the size of insects. Their small size condemned them to comparatively few brain-cells; and this limitation of the number of brain-cells made it impossible for them to provide all the myriad alternative brain-pathways which are needed for any elaborate process of learning and for the plastic behaviour we call intelligent. (It is perhaps no coincidence that several observers have remarked on the "insect-like" behaviour of the smallest warm-blooded vertebrates, the humming-birds.)

The construction of vertebrates, on the other hand, was admirably suited for strength, size, and power. All the biggest animals, both of land and water, are vertebrates. Thus when they had exploited to the full the mechanical resources of their bodies, there remained the resources of behaviour of which they could take advantage; for they could grow big brains, they could learn, they could adapt themselves individually instead of having to leave adaptation to the slow variations of the germ-plasm. Their size necessitated a longer growth; and this too favoured learning—and in its turn favoured longer life, so that experience should not be wasted. So the arthropods and the vertebrates represent two different lines of mental development. Chitinous armour and air-tubes limited their possessors to a reliance upon instinct: the vertebrates' tail and backbone, their general size and muscularity allowed them to develop their intelligence.

We ourselves are almost destitute of instincts. When people talk of human instincts they usually mean either habits or intuitions; and both habits and intuitions are based on years of previous experience. We find it very difficult to imagine the mental life of a higher insect. What can it feel like to be born with a nerve-machinery that ensures you shall react without prior experience and without education to quite

elaborate situations; to react to them in a finished and apparently purposeful way; and yet to be baffled by quite small variations in the situation?

What does it feel like, for instance, to be very hungry and yet starve to death rather than try any unaccustomed food outside the one species of animal or plant normally eaten, as many insects (but not a single vertebrate) will do? Or to be impelled, like some kinds of solitary wasps, to hunt for one kind of spider only, to sting it in a particular way so as to paralyse it, to wall it up with an egg as food for the grub which will hatch out of the egg—and then never pay any more attention to your offspring at all? What does it feel like to be able to build a honeycomb—a double plate of deep cells, the cells accurately hexagonal, the bases of all the cells of one plane elaborately dovetailing with those in the other? And all this without the least instruction in geometry or in wax-modelling? What does it feel like to be a worker-ant and know without being told exactly what to do with the babies of your own species; but to be so incapable of profiting by experience that if you are provided with ant-babies of another species which require a different food and different treatment, you never make the least effort to alter your routine and continue in your own ways although all your charges without exception sicken and die after a few days of your care?

The answer is that we do not know what it feels like; but that in all probability the level of accompanying consciousness is not high. Probably the insects do exceedingly little thinking; one object releases an elaborate train of behaviour, while another is paid no heed to, in the same automatic way that light of a certain wave-length hitting our eyes has to give rise to a reaction which we feel as a sensation of red, while light of only slightly longer wave-length cannot be perceived as light at all. The instincts of insects, however extraordinary, are for the most part nothing else but reflexes. The animal is turned out complete with the possibility of them, as a musical-box is turned out complete with the

possibility of playing a definite but limited repertory of tunes. Its behaviour is part of its inheritance; and just because it is so automatic, no more demands thought than does our withdrawal of a pricked finger from a needle, or the secretory activity of our pancreas when stimulated by secretin in the blood.

The insect has its repertory of inborn tricks. It does not have to learn them however elaborate; but in revenge the repertory is limited, and the tricks are so automatic that they easily fail in any unusual situation. The vertebrate has the trouble of learning by experience (which may be bitter), but in return it has a far greater range of possibilities open to it, a much more adaptable behaviour.

It is interesting to find that the same rigid and narrow specialist adaptation to a particular way of life is seen in other departments of insect life. This is particularly well marked as regards hearing. The ear of all higher vertebrates is sensitive to tones of a wide range of pitch; and from the enormous variety of sounds which the animal is thus enabled to perceive it picks out those which have meaning for it. Among insects, comparatively few have hearing-organs at all, and these, in some cases, are adapted to perceive only the particular note emitted by other animals of the species; their world of sound is confined to one or two tones.

We may reasonably assume that when an insect cannot satisfy one of its instinctive impulses it feels some sort of displeasure, and if it is thwarted, experiences something like anger at whoever is doing the thwarting; that it is somehow excited by the sight of its prey or the smell of its mate, and feels some kind of satisfaction in the proper accomplishment of the behaviour its instincts force upon it. But of anything like a train of thought, rational or not, it cannot be capable. And experience, even in the highest insects, can do little except to put a polish, so to speak, on the machine-made instincts already conferred on it by its hereditary constitution.

We can sum up this divergence between insect and vertebrate from another and rather different point of view.

Behaviour and mind, no less than bodily structure and chemical physiology, have all in the long run been evolved in relation to their environment. We need not beg a philosophical question and say they are determined by it, but at least they are conditioned by it. The very sense-organs, on whose information we depend to build up the highest flights of intellect or imagination, show this conditioning very clearly. No animal, for instance, possesses any sense-organ for detecting whether a wire or a rail is carrying an electric current or not; and yet such a knowledge is sometimes a matter of life or death. The reason for this gap in our repertory is doubtless the fact that powerful electric phenomena (apart from lightning, which cannot be avoided) do not occur in life's normal environment; they have only begun to exist in the last few decades. But had electric currents dangerous to life been running through the landscape during geological time, then animals, we can confidently assert, would have evolved sense-organs to detect them.

And the sense-organs which life does possess are narrowly conditioned by the facts of the lifeless environment. Sugar is abundant in nature, and sugar-containing substances are nutritious. Hence we not only possess sense-organs capable of detecting a sweet taste, but we find sweet things agreeable. Had the nutritious sugars been rare in nature, and saccharine, which is useless for food purposes, been abundant, the sensation of sweetness would doubtless not have been pleasant; while if lead acetate or sugar of lead, which is sweet but poisonous, had been the common sweet substance, sweetness would of necessity have been disagreeable to the higher animals, for only those with natures that found sweetness nasty would have escaped being poisoned. As final correspondence between sense-organs and environment let us mention the fact that of the energy which the sun radiates upon the surface of our earth, the maximum intensity is of the wave-length which gives us a sensation of greenish-yellow; and this is right in the middle of the narrow range of radiations (only a single octave of them) to which our eyes are

sensitive. If the sun were in a somewhat different stage of stellar evolution, and was sending out most of its energy in the form of orange or red rays, it is pretty certain that the range of radiation we can see would centre on red instead of on yellow. We should see other colours beyond the red, and we should be blind to blue and violet.

Organisms, in fact, are relative beings ; they have meaning in relation to their environment, no meaning apart from it. And this relativity of life is just as pervading in regard to the senses and the mind as it is in regard to the mechanical construction of a limb or the adaptive significance of a colour-scheme.

But arthropods and vertebrates differ in the way in which mind and behaviour are fitted to the environment. Your arthropod is born adapted. A lobster, for instance, is born with a veritable battery of tools growing out of its body—walking legs and pincers, jaws of various kinds, swimmerets—each capable of doing some special thing. Get hold of a lobster and see them for yourself, if you can. The arthropod mind is rather like that. Contrast your own hand with the lobster's organic tool-kit—it has no sharp edges or crushing forces, none of the special structures with which a lobster's limbs are so richly and variously provided. But it can move, plastically and adaptably, and be turned to a great variety of uses. Much the same can be said of your mind. It starts off comparatively unencumbered by special instinctive furniture, and adapts itself as you grow up by learning what to do. Your butterfly creeps out of the pupa-case in which it has shaped from an almost unorganized pulp. It brings with it two pairs of wings, six pairs of legs, two antennæ, and a highly specialized battery of mouth-parts ; most remarkable of all, it brings a brain finished and complete. It knows from the outset what it is to do and how it is to do it. It never grows up or learns ; it enters the life drama in fully adult form. Contrast your own first appearance.

Those two types, butterfly and man, present the contrast of arthropod and mammal in its extremest form. All arthro-

pods are mechanical as the butterfly is, but few vertebrates have a plasticity that even approaches our own. In studying the behaviour of arthropods we shall see how much is possible on the level of purely mechanical behaviour. Later, when we turn to vertebrates, we shall trace the gradual supersession of inflexible instinct by a new and more effective kind of mental organization.

§ 2

An Anatomy of Instinct

The complication of the actions which insects perform untaught, and in the absence of all experience, has struck observers from the earliest times; and it was the study of insect behaviour which played the dominant rôle in generating the concept of instinct which prevailed both in biology and in general thought for the best part of the eighteenth and nineteenth centuries. The concept was also modified by philosophical and theological notions, it being almost universally held, before the evolutionary idea came into prominence, that the actions of man were guided by reason, those of animals by a wholly different faculty called instinct, directly conferred upon them by God. How erroneous is the first part of this antithesis will become apparent in full force when we study human behaviour; and the last half-century's detailed studies of animals have made it increasingly dubious whether the very term instinct should not be discarded.

Addison reflected the general view of the eighteenth century when he wrote in the *Spectator*:

> I look upon instinct as upon the principle of gravitation in bodies, which is not to be explained by any known quantities inherent in the bodies themselves, not from any laws of mechanism, but as an immediate impression from the first Mover and the Divine energy acting in the creatures.

To us, with the evolutionary idea as background, the facts of nervous physiology as foundation, a radically different approach is necessary.

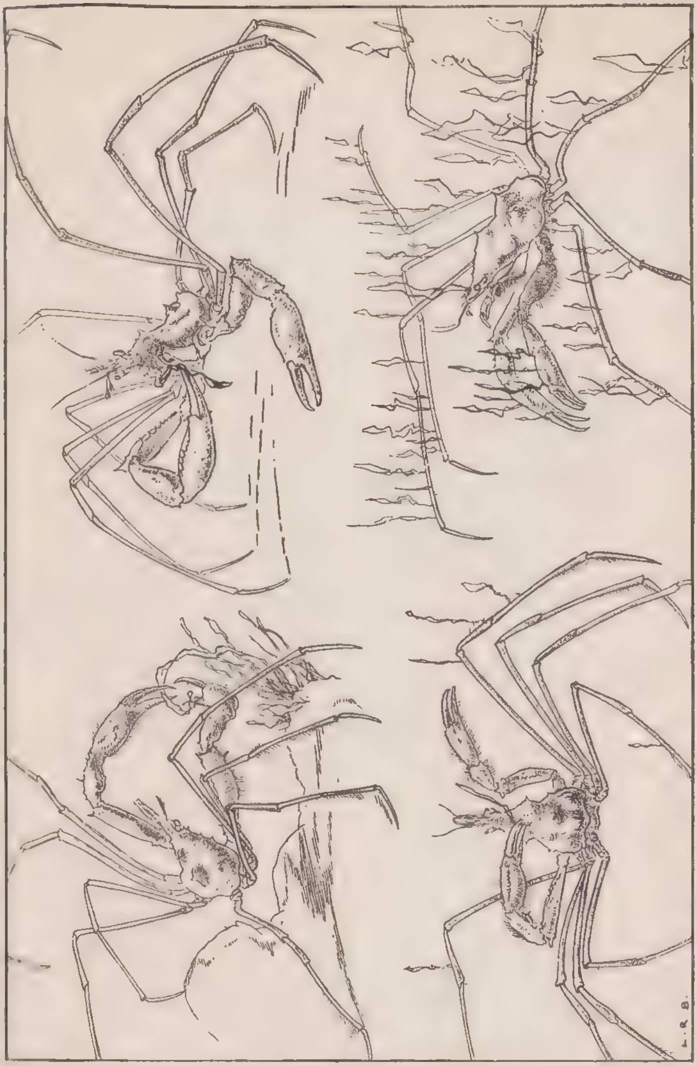


FIG. 17.—AN ELABORATE INSTINCT.

The spider-crabs disguise themselves by picking bits of weed, biting them off to the right length, and attaching them on to the little hooks with which their backs and claws are covered. It has been shown by experiment that the action is purely instinctive.

Let us take one or two examples of what are commonly called instincts. One of the most illuminating is the spinning of a cocoon by caterpillars about to pupate. They have never seen their parents or a cocoon belonging to their species; they cannot know by any form of experience that they are suddenly going to pass over into a passive pupa, with all their old organs in a state of dissolution; nor that they will emerge from this second period of embryology as a winged insect which must escape from the cocoon and will have only a tongue, no jaws to bite its way out.

And yet, what elaborateness of apparent precision! The cocoons of the moth *Saturnia pavo*, for instance, protect the pupa by being exceedingly tough; to make it possible for the winged adult to get out, the substance is fitted with an arrangement of spikes like that in a lobster-pot, but leading the other way, allowing egress and not ingress. Addison, confronted with such a cocoon, would doubtless have said that God had conferred upon the caterpillar a knowledge of the mechanical principles involved in lobster-pot construction.

In an attempt to become more scientific, many naturalists later abandoned the view that the knowledge had been implanted by the Creator, in favour of the idea that instinctive actions were inherited habits. Previous generations had once done them consciously, deliberately, with effort; the actions became gradually perfected, but at the same time more automatic, until they were done with the same effortlessness as that with which we achieve such difficult but habitual tasks as talking or writing.

But this view is untenable. For one thing, it demands the inheritance of acquired characters if it is to work, and that, as we have fully set forth in the fourth Volume of this Series, is something which in all probability does not happen. But even if acquired characters were inherited, matters would be little better. For no one can seriously suppose that a caterpillar, for instance, can possibly know that he or she is going to wake up one day as a winged butterfly, and can have the foresight to make provision for this future event. It can

never have done its spinning work consciously and deliberately, because it can never have possessed the facts on which to deliberate.

The impossibility of there being knowledge behind instinct is perhaps most prettily illustrated in the well-known case of the yucca plant and its moth, *Pronuba*. The yucca, or Spanish bayonet, with its lovely spikes of white bells, can only be fertilized by the help of this particular moth. The female moth visits the yucca flowers (each of which stays open only for one night), scoops up the pollen, which is rather sticky, and kneads it into a pill, which she holds in a pair of specially shaped appendages. Then she pierces the ovary of the flower with her long ovipositor and lays three or four eggs just between the future seeds. And then, flying up to the pistil, she pokes the pollen-ball down into the cup which it conveniently bears at its tip, and leaves it sticking there. She then repeats the process with another flower. The pollen germinates, sends down its pollen-tubes, fertilizes the plant's eggs, and the caterpillars that meanwhile hatch from the moth's eggs begin to eat the seeds. As there are about two hundred seeds in one flower, and as each of the three or four caterpillars needs about twenty-five seeds, almost half are left over for the needs of the plant. The full-grown caterpillars eat their way out of the seed-capsule, let themselves down to the ground by a silk thread, and make themselves a cocoon there ; without eating any more, they await the transformation to a pupa, which does not overtake them until the next summer ; and later in the season they emerge as moths, to mate and repeat the cycle.

The association is one of mutual benefit, a reproductive symbiosis ; the action of the female moth in putting the pollen-ball on the pistil seems admirably purposeful, just as her care not to kill the goose that lays the golden eggs, by only introducing three or four future grubs into each flower-capsule, seems admirably calculated. But when we reflect that the mother moth dies before the seeds mature, and that the moths of the next generation have never seen a yucca in

flower before they begin their business of pollen-gathering and egg-laying, it becomes obvious that foresight and reason can play no part in the instinct—quite apart from the fact that experiments have decisively shown that no insect is capable of drawing such conclusions as the moth would have to draw if it were really being intelligent on the facts presented to it. We have no more right to suppose that the moth is being purposeful and intelligent in its actions than that the yucca is being purposeful and intelligent in growing a pistil with a cup at its tip to receive the pollen; or, to confine ourselves to the moth, we have no more reason to find proof of intelligence in its actions in putting the yucca pollen in the proper place than in its growing the special appendage with which to manipulate the pollen.

There we have the gist of the matter; an instinct is, like a leg or a gland or an adaptive colour-pattern, one of the tools of the species; it merely happens to be a bit of behaviour-machinery instead of a bit of engineering or chemical machinery. It is the outcome of the animal's nervous construction, as the leg and its working is the outcome of its mechanical construction. It is a bit of nerve-clockwork.

As such, instincts can be polished up, altered, specialized by the same evolutionary agencies as limbs or glands. If we believe that natural processes, such as variation and selection, can account for the existence of adaptive structure or colours, we need have no difficulty in thinking that the same processes can account for adaptive instincts.

In the same way, the leaf-insect does not say to himself: "Every day in every way I will look more and more like a leaf"; or the bug that grows a sham ant on its thorax deliberately pretends to be an ant. That was all worked out for it by the forces that mould the species no more and no less than were the levers of our arm-bones or the light-focusing apparatus of our eyes. In fact, the ant-bug has got such poor eyes that it is probably quite incapable of forming an image of an ant nearly as accurate as the imitation he grows on his thorax. It is the sharp eyes of the birds that have ensured the

bug's likeness to the ant, not any volition or intelligence on his part.

Nor is there any more proof of intelligence in the behaviour that goes with the colour to make it protective. The young plover that at the sign of danger crouches down on the shingle into invisibility will do the same on a carpet or a lawn where it is extremely conspicuous. The stick-insect will stiffen into the resemblance of a twig whenever it is illuminated, and stay thus rigid so long as it is illuminated—and this whether it is among twigs, or on the laboratory bench, or exposed to the eyes of its enemies on an open path. The mother bird that trails one wing as if wounded in front of an intruder is not deliberately simulating injury; she is carrying out an inborn method of response.

Here the curious fact (already mentioned on p. 45) that prawns will creep to the positive pole if a weak electric current passes through their tank, is illuminating. Obviously there is no advantage in their going to that pole. Under natural conditions such circumstances never arise; it may be said with certainty that no more than a few hundreds of prawns out of the myriads that have lived on earth have ever had an opportunity of exhibiting their galvanotropism. Yet the phenomenon depends on a property common to all prawns—upon the way the nerve-fibres happen to be arranged in their central ganglia. It is a necessary consequence of their anatomy. The instincts that we are discussing are really only more complicated instances of the same kind of thing; the animals are so made that, given a certain combination of circumstances, they will—and must—behave in a certain way. The only difference is that the instincts which are useful to their possessors have been rendered adaptive through the agency of Natural Selection. Just as the colouring of a leaf-insect or a young plover depends on the way its pigments are disposed, so the actions of a cocoon-spinning caterpillar or of a female yucca moth depend on the way their inner protoplasmic telephone system is planned.

The absurdly automatic nature of insect behaviour is well

illustrated by the mating reactions of certain moths in which the males smell out the female by the aid of their huge feathery antennæ. So acute is their sense of smell that males will come from more than a mile away to flit round an empty box in which a female has been confined. If a male be put with a female in a cage, mating will follow in due course. If the male's antennæ be cut off, however, he is incapable of recognizing the female as such—or rather, his antennæ are the one channel through which the mating reaction can be stimulated, so that without them his sex-behaviour cannot be set going. Most remarkable of all, however, is his reaction to the two little scent-organs which the female possesses near the tip of her abdomen. If these be cut out (an operation which does not seem to incommode the female) and they and the operated female are put in a cage with a normal male not deprived of his antennæ, he will pay no attention to the female, but will make vain attempts to mate with the two little scent glands. It is all so different from human reactions that we can scarcely grasp it. But if we want to understand the world of insects, we must try to grasp it. We have to realize that the male moth has no idea of a mate; he merely possesses mating reactions; and these are fired off by one stimulus and one only—a particular smell.

When a bee stings, a similar automatism is revealed. The actual mechanism of stinging is purely reflex. If a worker-bee stings a man, it leaves its sting in the wound; and the isolated organ there continues to execute the same movements as during the first piercing of the skin, so piercing deeper into the flesh. When the experienced bee-keeper is stung, he therefore makes haste to extract the sting at once. This reflex machinery is, however, normally held under higher control. A bee whose brain has been extirpated, has had its chief inhibiting centre removed; and it puts itself without ceasing through its various reflex paces, cleaning itself, protruding its sting, walking restlessly about, fanning its wings, and so forth.

Higher vertebrates have instincts just as much as insects. But in them, the instinct is rarely so machine-made; it is

flexible at its two ends, both as regards the situations which call it out and the methods adopted to execute it. And the process continues until in man nothing is left but the most central part of the instinct, the instinctive impulse like fear or attraction or anger which pushes one on to act in a certain general way when confronted with a certain general kind of situation. Nothing approaching this flexibility is seen in any insect. Men have trained performing fleas ; but the fleas are merely crawling or hopping along in the ordinary way while harnessed to a miniature carriage. No one could train a flea or any other insect to do anything so different from its ordinary activities as shamming dead or jumping up at the word of command, like a dog, or bicyling, like a performing bear, or sitting up at table and politely passing the plates like the young chimpanzees at the London Zoo. Insects have elaborate instincts because they have no elaborate brains to be intelligent.

This lack of intelligence is most clearly seen in those numerous instances in which an instinct, beautifully adapted to the ordinary conditions of the possessor's life, makes default and even acts wastefully or harmfully, when the conditions are changed—even though the least glimmer of intelligence would have set matters right.

In one species of solitary bee, each mother builds a mud cell which she fills with honey and pollen up to a certain level ; then she lays an egg on the food ; and then seals the cell up. An observer broke upon a cell while the bee was away. On her return, she noticed the hole, for she explored it thoroughly with her antennæ. But she had not the sense to mend it. She proceeded with her business of food-gathering, load after load of food being deposited in the cell only to fall through the open hole. When she had brought the regulation number of loads, she laid an egg, and sealed up the foodless cell. As with the solitary wasps we shall shortly describe, the normal behaviour is a chain of actions, each determined by the one before, each determining the one after. It is adaptive, but not purposeful.

An even more obvious example of clockwork instinct is

provided by certain cocoon-spinning caterpillars. If the animal is interrupted in the middle of its task and the half-finished cocoon removed, it will not begin again from the beginning, but will spin only what remained for it to do, in spite of the fact that the half-cocoon it produces is completely useless for protection.

Forel describes how, when a battle is raging between different kinds of ants, you can decapitate two of the combatants, and the heads will go on trying to fight each other for some minutes. That perhaps depends as much upon the fact that insects get their oxygen by air-tubes, and not in blood, as upon the reflex nature of their behaviour. But what are we to think of the worker-wasp who was imprisoned with a grub of its own species, but without food? It wanted to feed the young wasp, but was in evident perplexity how to do so. Eventually it bit off the grub's hind end, and offered it to the front end.

There we may leave our anatomy of instinct. We shall describe a great variety of insect instincts in subsequent sections; but they are all variations on the same theme; they are all behaviour which is in the main the rigid outcome of inherited nerve-structure. We should find the same machinery of behaviour at work in other groups. There are the hermit-crabs which have the instinct to find shells as houses for their unprotected abdomen, the other crabs which go about, one sort with stinging sea-anemones held as knuckledusters in its claws, another sort with a distasteful garlic-smelling sponge. There are the octopuses which have the instinct to build themselves a little den of stones, behind which they can lurk unseen; but if you give them bits of glass, they will build their rampart as readily with them, although it is transparent and lets its occupant be seen. There is the elaborate flight-instinct of the squid, with its ejection of ink and a right-angled turn at the crucial moment. There are the instincts of spiders, which rival those of insects in their elaborateness. The combination of structure with appropriate instinct is beautifully seen in a burrowing spider,

whose abdomen ends behind in a hard flat plate; it uses this as its front door to block the entry to its burrow. There are the web-spiders, which build their wonderful snares without ever being taught; the common garden spider usually builds two new nets a day, one in the morning and one in the afternoon, for its many weeks of life.

But it is in the Hymenoptera, the ants, wasps, and bees, and in the termites, that rigid instinct attains its highest levels of intricacy. First we will consider the very interesting mechanism of the solitary wasps and then pass to the complex interplay of the social insects.

§ 3

Solitary Wasps

Most wasps are solitary; only a few are social. You may read an excellent account of their ways in G. and E. Peckham's *Wasps*, or (together with many other vivid and illuminating descriptions of insect behaviour) in the works of Fabre.

The almost universal characteristic of solitary wasps, out of which the social habit has evolved, is their provision of food for their young. And though the adults live mainly or solely upon fruit or the nectar of flowers, the growing grubs are universally carnivorous. In solitary wasps there are no neuter workers. The males have but one biological duty—to impregnate the females. The females, once charged with a store of sperms, make burrows in the ground or in walls or tree-trunks. They then hunt for prey, which may be spiders, caterpillars or ants, flies, moths, plant-lice or other arthropods, and sting them through the nerve-centres in their nerve-cords, a procedure which kills in some species but which usually paralyses without killing. The paralysed prey is then put in the burrow, and an egg laid on it or beside it. In most cases the burrow is then sealed up and abandoned, so that the parent makes provision for an offspring it will never see. Each species of solitary wasp—and there are many hundreds—chooses a particular kind of situation for its nest,

hunts only one kind of prey, and makes and seals its burrow in its own characteristic way.

All the wasps of the genus Ammophila, for instance, confine themselves to caterpillar-hunting. They first make a nest in the soil. Then they seal it up with sand, take a flight round to fix the neighbourhood in their memory, and depart to hunt for caterpillars. This is not a light task. Although the wasps spend most of their time running up and down likely plants examining the under-sides of leaves, they rarely find more than one victim a day. When the victim is found, it is stung and paralysed. The stinging is an elaborate business; we will quote the Peckhams' account of one wasp they watched in the act:

> The wasp attacked at once, but was rudely repulsed, the caterpillar rolling and unrolling itself rapidly and with the most violent contortions of the whole body. Again and again its adversary descended, but failed to gain a hold. The caterpillar, in its struggles, flung itself here and there over the ground, and had there been any grass or other covering near it might have reached a place of partial safety; but there was no shelter within reach, and at the fifth attack the wasp succeeded in alighting over it, near the anterior end, and in grasping its body firmly in her mandibles. Standing high on her long legs and disregarding the continued struggles of her victim, she lifted it from the ground, curved the end of her abdomen under its body, and darted her sting between the third and fourth segments. From this instant there was a complete cessation of movement on the part of the unfortunate caterpillar. Limp and helpless, it could offer no further opposition to the will of its conqueror. For some moments the wasp remained motionless, and then, withdrawing her sting, she plunged it successively between the third and second, and between the second and the first segments.
>
> The caterpillar was now left lying on the ground. For a moment the wasp circled above it, and then, descending, seized it again, farther back this time, and with great deliberation and nicety of action, gave it four more stings, beginning between the ninth and tenth segments and progressing backward.

After this she gave herself a thorough toilet; and then proceeded to bite at the neck of her victim, pinching it repeatedly between her strong mandibles.

The paralysed caterpillar, though much heavier than the wasp, is then dragged across country, through jungles of

grass-stems, to the nest, which has been previously sealed up. One wasp was watched dragging its prey nearly a hundred yards, which took over two hours. When the nest is reached it is opened, the prey pushed in, an egg laid on it, and the nest-opening carefully sealed up again. A second caterpillar is usually brought later to the same nest, as one is not enough for the young grub.

Fabre had described his French Ammophilas as stinging their prey with an uncanny precision which could only mean that they possessed in some mysterious way a knowledge of caterpillar anatomy. The wasp's sting, he maintained, always pierced the caterpillar's nerve-centres (of which there is one in every segment) in such a way that the victim was completely paralysed, and thus could neither wriggle and crush the young wasp-grub, nor die and decay. And his statements are still often quoted as examples of the unerring and supernormal revelations of instinct. But the careful observation of the Peckhams has shown that Fabre was here at fault, or at least that the conclusions he drew are not in the least general. In the American Ammophilas the stinging is much more variable, both in execution and results, than he records. The instinct of the wasp, it seems, is simply to thrust its sting into the lower surface of the caterpillar (the sting goes in most easily at the joints between the segments of the body), and to go on doing so at different places until its victim becomes more or less limp. Sometimes the wasp is content with a single sting, sometimes it stings the caterpillar between all of its thirteen segments.

And not more than half of the stung caterpillars observed by the Peckhams lived on in a paralysed state. Some of them reared and rolled about violently when the wasp-grub began to take mouthfuls out of them ; others died quite soon and became decomposed before the wasp-grub had finished its growth. In both cases, however, the grub's development was not prevented. So long as the victims are not fully active, and so long as most of them do not decay prematurely, the method will work. The quasi-miraculous accuracy of

the wasp's surgery turns out to be a rough-and-ready reflex of no great complexity or regularity: the wasp has no surgical knowledge of the insides of caterpillars, but merely displays a reaction to the feel of their bodies. The same simplicity of behaviour is seen in those species that provide spiders for their grubs: they react to captured prey by thrusting their sting into the lower surface of the spider's fore-part. As the nerve-centres of spiders are concentrated in a single mass surrounding the gullet, the sting will in nine cases out of ten pierce some part of this compound centre and so achieve some degree of paralysis.

The instinctive and machine-like quality of most of their behaviour was clearly shown by some experiments of Fabre on the wasp Sphex, which hunts crickets. When the Sphex has brought a paralysed cricket to her burrow, she leaves it on the threshold, goes inside for a moment, apparently to see that all is well, emerges, and drags the cricket in. While the wasp was inside, Fabre moved the cricket a few inches away. The wasp came out, fetched the cricket back to the threshold, and went inside again—on which Fabre again moved the cricket away. He repeated the procedure forty times, always with the same result; the wasp never thought of pulling the cricket straight in. Drag cricket to the threshold —pop in—pop out—pull cricket in: the sequence of actions seems to be like a set of cog-wheels, each arranged to set the next one going, but permitting of no variation. The Peckhams repeated the experiment with an American Sphex. This creature was not quite so automatic, for after her prey had been moved a number of times, she did drag it straight into the burrow.

These wasps have a certain power of learning, as shown by their memory for the surroundings of their nest: and some of them at least can modify their behaviour in a way which shows the beginnings of intelligence. But the main flow of behaviour is automatic. All that experience does is to change a detail here and there: and the change is made as it were under protest, and only after many repetitions.

The same cogging up of behaviour in a rigid sequence of actions was found by the Peckhams in *Pompilius quinquenotatus*, one of the spider-hunting wasps, which has the instinct to hang its prey in the crotch of a grass-plant. This species only digs a burrow after catching its spider, and the hanging up of the prey serves to keep it from being stolen by ants while the wasp is busy digging.

If a paralysed spider is removed from the crotch where the wasp has hung it, and an uninjured spider substituted, this latter will usually remain quiet for a time, as it reacts to handling by "shamming dead." The wasp comes back in due course, and in some way notices the difference. But instead of stinging the new spider, she refuses to have anything to do with it (this is not due to the spider having been handled, as was readily shown by experiment), and flies off to find another. When she comes back with the new prey, instead of using the burrow she has just made, she digs another. Here again an invisible sequence must, it seems, be preserved. Only a paralysed spider in a grass-crotch releases the reaction to drag the prey into the next. An unparalysed spider in a crotch is not a normal phenomenon, and interrupts the whole chain. Similarly, the hanging up of a paralysed spider provides the stimulus for the next action in the sequence, the digging of the burrow; and this is called out, even if a perfectly good empty burrow is waiting.

Among individuals of a single species there is a good deal of variation in instinct, just as there may be in colour or size; but in a single individual the instinct is, within very narrow limits, fixed and rigid.

§ 4

Insect Societies

We come now to the most interesting aspect of arthropod behaviour, the formation of co-operative communities of insects which store food and have a real economic life.

The incipient stages of sociality, in which parents remain

with and look after their young, are to be found here and there in many orders of insects, such as earwigs and some beetles. But true social life, in which the young stay on with their parents and help with further broods, is known in two groups only. One is the Hymenoptera, which includes ants, bees, wasps, and ichneumons. The other, the Isoptera, a very different order allied to the cockroaches, consists of the ermites, often miscalled white ants.

But there is a still further degree of insect social life. Some of the young may be transformed into unsexed neuters, who take upon themselves all the duties of the colony except that of reproduction.

The ants are the most specialized and the most successful of all social units. We will begin with some account of them, and then pass to the termites as a remarkable example of parallel independent evolution. We shall next deal, very briefly, with some interesting facts about bees. The social wasps, a further variant of the social theme, will demand no more than incidental mention.

All ants, like all human beings, are social animals. Many people seem to imagine that ants are like miniature men—that there are a number of ant races and peoples, some practising one mode of life, some another, but all part of one big single group. This is very far from being the case. There are over three thousand five hundred separate species of ants already known to science, each one a biological unit pursuing its own independent path, incapable of interbreeding with any other.

These various species show an extraordinary diversity of size and structure. The largest worker-ants weigh about a fiftieth part of an ounce—four or five thousand times as much as the smallest. There are some worker-ants with formidable grinding mandibles for chewing up grain, others with sabres for piercing their enemies' heads, others with leaf-cutting scissors for jaws. There are those with huge heads and those with tiny heads, those with squat bodies and those with slender bodies. For we must not forget that, in striking

contrast with men, ants have to be built for their jobs. They do not make tools; they grow them as parts of their bodies. Almost all ants, for instance, have an antenna-comb, an ingenious gadget for holding their sensitive antennæ and combing them free of dirt, which is built into one pair of their legs. Two or three kinds of ants have huge heads expanding to end forwards in a round, flat, hard surface. These creatures station themselves at the entrances to the nest, which they block completely with their heads, moving aside when another worker taps them with its antennæ. They are porters and doors in one.

Each species of ant is thus built specially for its own particular kind of life and is quite unadaptable to any other. Even within the single community there is the same kind of specialized physical diversity. Only the males and females have wings; the neuters grow up wingless. The neuters have much bigger brains than the males or the queens; but, as they never have to fly, their eyes are smaller. In an ant called Carebara, the neuters are minute; they are only about one-thousandth of the bulk of the queen. It is as if Lilliput were not only sober reality, but as if Lilliputians lived side by side with normal-sized men and women to make up a single human community.

Even within the neuter caste there may be markedly different sub-castes. Contrasted with the more ordinary-looking workers, there may be soldiers, larger, with portentous heads, and battle-axes for jaws. In such creatures as Atta, the leaf-cutting ant, there is a huge range of neuter size and structure. In this genus we can if we like distinguish soldiers, worker majors, worker minors, and the tiny worker minimæ; but the different forms are actually connected by every possible gradation. In more specialized cases, soldiers and workers may be sharply marked off from each other, with a gap between.

This physical diversity goes hand in hand with diversity of behaviour. The males do nothing but fertilize the queens when the times comes. The queens lay eggs unceasingly.

The workers have the instinct of tending the young, the soldiers are impelled to bite and snap in defence of the colony. The workers of one kind of ant keep ant-cows, but never look at grain or make raids on other ants. Those of a second are only graminivorous, those of a third live by slave-labour. Thus the division of labour in an ant-community, unlike the division of labour in a human community, is based on marked, inborn individual differences of structure and instinctive behaviour between its members.

The way in which the ant-stock exploits the resources of the world is equally different from the human way; it does so by splitting up into thousands of separate species, each with its own inborn peculiarities, instead of remaining one species with branches differing only in their acquirements of tradition and culture.

The neuters of ants, bees, and wasps are not a third sex; they are sterilized females, which develop with rudimentary ovaries and oviducts. The difference between them and the fertile females, the queens, seems to be brought about solely by feeding. This we know for certain in bees. Female bee-grubs fed on "royal jelly," which contains more pollen and therefore more protein, grow into queens, those fed on a less protein-rich diet grow into workers. The constitution of the female bee is so devised that it has these two possibilities of expression to be unlocked by the keys of two different diets.

Bees have only one sort of worker, but among ants further differences obtain, giving soldiers and workers of different types. While the difference between queen and neuter seems to be due to a difference in the quality of food, that between worker and soldier depends apparently on differences in quantity. Where there exists a gradation between worker and soldier, we find that the proportionate size of the head goes up with the absolute size of the whole body, just as happens with the big claws of lobsters and many crabs. The developmental machinery is so set that keeping the grubs underfed and making them pupate when quite small will lead to a creature with relatively tiny head, while fattening them

to the greatest possible size will mean that the neuter into which they metamorphose must not only be big but big-headed.

The difference between female (whether neuter or queen) and male, however, depends on heredity. But the method of sex-determination is different from the normal. Instead of the male having one chromosome less than the female, he has a whole set of chromosomes less; for he arises from an unfertilized egg.

The eggs of these social insects are unique in the animal kingdom, for they will develop equally well whether fertilized or no; they can be parthenogetic, but do not need to be. Unfertilized eggs always turn into males, fertilized into females. Whether an egg shall be fertilized or no is controlled by the queen as she lays it. The queen, in bees and wasps as well as in ants, mates once only in her life—during her "nuptial flight." The population of spermatozoa she then receives is stored in a little purse, opening off the oviduct, with purse-strings of muscle round its neck. In this they live for all the rest of the queen's life—a period that may extend to several years; seventeen years is the longest recorded. If an egg is to grow into a female, the sphincter is relaxed an instant as the egg passes across the bagful of sperms, a few sperms escape, and one fertilizes it. If it is to grow into a male, the sphincter is kept tight shut, and the egg pursues its parthenogenetic way.

There is a reason for this. The ordinary methods of sex-determination inevitably give equal proportions of males and females. But the states of ant, bee, and wasp are based on the labour of sterilized females. What should they do with a huge population of useless males, when a few more score are ample to perpetuate the race? The problem has been neatly solved by the adoption of this other method, in which the proportion of the sexes can be varied as required.

The way an ant-community develops is as follows: Swarms of winged males and virgin females fly out of their nests (leaving an excited population of workers round the

doorways) and up into the air for the only flight of their lives. Nuptial hordes issue at the same time from all the nests over a large area ; this simultaneous flight is prompted apparently by special weather conditions, and certainly promotes cross-fertilization between different nests. Queen ants differ from queen bees in permitting several males to mate with them, one after the other. When this polygamous flight is over, the males drift off to perish of starvation. Of the females, some return to their old nests (for in ant-societies many fertile queens may live and lay in mutual tolerance within a single nest) ; others fail to find their way home, and proceed to found new colonies. They find a sheltered spot, creep in and break off their wings at a pre-formed plane of weakness. For weeks they take no food, but live, ripen their first eggs and feed the first batch of young grubs at the expense of the material produced by their degenerating wing-muscles. The first grubs pupate and turn into workers. These at once, without any instruction, take over all the duties of the nest-building galleries, keeping the place clean, and tending the young. From now on the queen does nothing whatever for the community but lay eggs.

In bees and wasps the nests are often beautifully regular, and always contain rows upon rows of developmental cubicles for the young. Every member of the colony lives boxed up in his or her or its private cell from first egghood to adult emergence. But in ants the nests, often subterranean, consist of an irregular network of galleries and chambers, and they never contain special cells for the grubs. Ant-homes thus lack a certain picturesqueness to be seen in the hive, but in both respects the ant is really more advanced than the bee or wasp. The irregularity of the nest allows much greater plasticity, more freedom in adjusting means to ends ; and the young, not being confined to one spot, can be taken from chamber to chamber as conditions demand, or even given an airing or sunning out of doors.

What interests us most of all, however, is to find what keeps the ant-community together, how its social and

economic life is organized and unified. In human societies there is an economic nexus, of goods and services and money ; there are sentiments of patriotism and social devotion ; there is education at home and at school, to fit the growing child for his life as a social being and to train him for a particular career.

It is wholly different with the ants. Among them there is no education. The workers, it is true, can learn to modify their behaviour to cope with certain unaccustomed situations, but the modification is slight, and when the shroud-like covering of their pupal life is stripped off them by their nurses they emerge fully equipped with the instincts needed to carry on with the work of nest-building and food-gathering and nursing. They can learn their way through quite complicated mazes, but their learning is slow and stereotyped compared with that of vertebrates. The division of labour, again, which in human communities is the result of special training, is, among ants, the immediate result of inborn differences in structure and instincts.

Then ants have a sort of patriotism ; but it seems to be based entirely upon smell. Ants which by some means or other have acquired the characteristic nest-smell are tolerated and treated as fellow-citizens ; those which have not this shibboleth, even if they belong to the same species, are attacked and killed. By putting a number of pupæ of different kinds of ants together, an artificial mixed ant-state can be produced. The animals on emergence all acquire the same smell and live together in amity, though in nature they would fight to the death. Blood is thicker than water ; but for ants at least smell is more powerful than blood.

Ants can communicate with each other by means of their antennæ. But their communications are not of the nature of true language : they are of the same essentially reflex nature as those of bees, described in § 8 of this chapter.

Ants have an economic life, too ; this is based entirely upon direct exchanges of food. If you watch ants in an observation nest, you will often see one ant go up to another

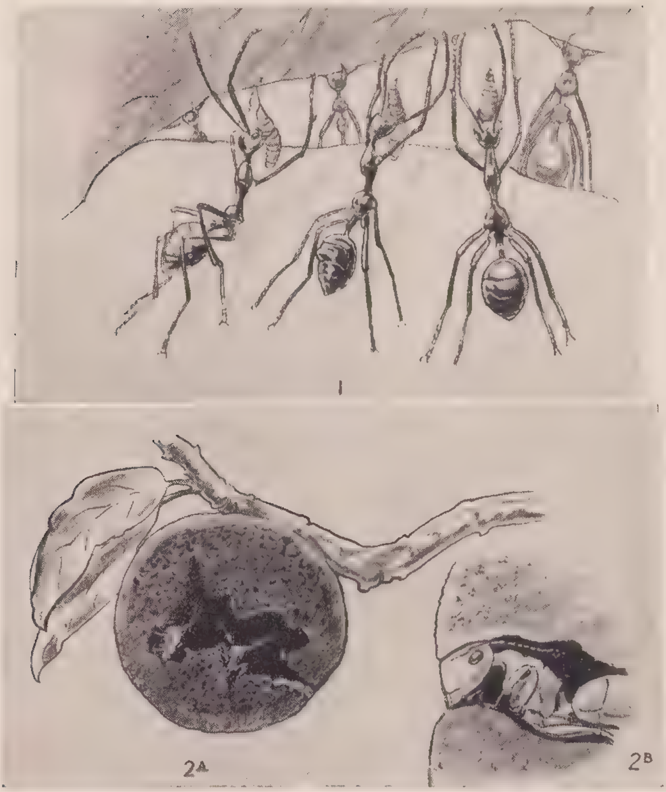


FIG. 18.—SCENES FROM ANT-LIFE.

(1) Workers of the ant Œcophylla repairing their nest. The nest is made of leaves. One set of workers is pulling the two sides of the rent together, others are using grubs as seccotine-tubes to stick the leaves together. (2A) Colobopsis at home. This Texan ant makes its nest in live-oak galls, 1 to 1¼ inches across. One gall is here represented as if cut across. A soldier is using its head to plug the entrance (below on the right). (2B) A "porter" soldier enlarged to show how its head is modified to serve as a door.

and stroke it with its antennæ. This is a solicitation of food. If the second ant is well-fed, it will stop; the two will raise the fore-parts of their bodies until their mouths are close together, and the second ant will produce from its mouth a drop of liquid which the other will swallow.

This liquid it pumps up from its crop, a large reservoir in the front of its abdomen, between gullet and true stomach. Forel calls it the "social stomach," because any food which it contains is part of a common store, available for any other ants which come begging. Only when food passes the valve from crop to true stomach is it digested and utilized by the private individual. When honey coloured blue with a harmless dye is given to ants, the blue crop can be seen through the thin parts of the abdominal walls. If a few ants are fed on such dyed honey, within a couple of days practically every ant in the community will show a pale blue tinge, showing how vigorous is the exchanging of food. There is in fact a circulation of food within the colony very nearly as essential as the circulation of blood in the human body; and the altruistic instincts of the separate members of the colony are reinforced by the tangible economics of food-services rendered and received. Each particle of food is probably swallowed and regurgitated half a dozen times or so before it finally passes to be digested; since ants appear to have the sense of taste well developed, this will multiply six times the collective pleasure they derive from food.

All social insects have some system of food-exchange. In ants and bees it is confined to a passing of crop contents from mouth to mouth. In termites it is more elaborate, for food is exchanged in many states and forms. Some of the food is regurgitated, as in ants; but this fraction is only partially digested. More fully digested food is dispensed at the anus. As with the ant-cows, which we shall describe in the next section, only part of the assimilable substances are absorbed in the passage through the animal's own gut; the rest is passed out behind for others' consumption. Then some of the food which is digested and absorbed is worked up in the so-called

salivary glands into a nutritive liquid which one termite will produce for another's benefit. And some castes at least exude fatty substances from their skin, which are not only agreeable, but enable the different castes, in the unending darkness of the nest, to recognize each other by their taste. The difference between the food-exchanges of ants and termites is like the difference between a monetary system with only one kind of currency, like cowrie shells, and one with copper, silver, and notes.

In wasps we get an interesting variation. There is no exchange between adult and adult, but there is between adult and young. After a worker has fed a grub, it taps its head and the grub gives out a drop of slightly sweet liquid from its salivary glands, which the worker eagerly licks up. This difference from ant or bee practice is connected with wasp diet, which is mainly flesh. The growing grub needs protein for its growth ; the adult wasp needs chiefly sugars and suchlike fuels for its muscles. The grub, by returning part of its food in the form of sugary liquid, not only provides a bribe to keep the worker at its nursemaid work, but helps in distributing the available food economically. Sometimes the workers cheat, and try to get the grub to produce the sweet bribe without feeding it. Occasionally they succeed ; but for the most part the system works as an economic system should, to encourage legitimate business.

§ 5

Ways of Life among Ants

The ways of ant-life are various in the extreme. Most of their species are general foragers, picking up what miscellaneous small animal prey they can find. But there are many which have specialized. Certain ants, unique among subhuman animals, keep domestic animals. Man, a vertebrate, domesticates other vertebrates ; ants domesticate other insects. The commonest ant-cows (as Linnæus first dubbed

them) are plant-lice or aphids, but coccids or scale-insects are also kept. We keep cattle in order that they may transform grass, inedible by us, into edible milk and meat. The ants keep plant-lice and coccids to tap the liquid resources of the plants. No ant has developed sucking mouth-parts; their jaws are all built on the biting plan. They cannot therefore get at the rich currents of plant-sap. Aphids and coccids, however, have a proboscis designed for this purpose; they sit tight, anchored by their tongues, and pump themselves full of nutritive liquid. They are, however, wasteful in their internal arrangements. Much of the nutriment remains undigested, and is passed out in the form of little drops of sweet liquid, so-called honey-dew. Ants have always had a reputation for thrift, and they do not tolerate this waste. They lick the sugary mess off the leaves; or they catch the drop as it emerges from the aphis; or, last stage of all, they "milk" their cows, caressing them abdominally with their antennæ, upon which the ant-cows void their liquid contents.

The more specialized among pastoral ants really domesticate their insect-cattle. Some build little wood-pulp stables over them, and may connect the stables with the nest by covered passages. Others excavate underground chambers and set their cattle to exploit roots. And some tend the aphis eggs through the winter and put them out on plants when they hatch in spring.

Then there are the agricultural ants. In these, the larger workers climb trees, cut bits out of leaves, and bring them home held aloft like green umbrellas; in the nest they are chopped up fine and turned into regular beds of leaf-mould by the smallest workers. On these beds, which are suspended from the roofs of special subterranean chambers, the ants grow a fungus, a white meshwork of filaments. This, if left to itself, fruits in the form of a large toadstool. But so long as the ants have it under cultivation, it never fruits. They plant it on the chewed-up leaves, they weed the beds of other moulds, they manure them with their own excrement, and they treat the precious vegetable so that it grows in a peculiar

FIG. 19.—SCENES FROM ANT-LIFE.

(3) The beginning of a colony of wood-ants. A queen after her nuptial flight has broken off her wings, imprisoned herself in an underground cell, and laid her eggs. Of the grubs that hatch out she gives one much more food than the rest, in order that she may have a worker to assist her as soon as possible. (4) A queen Carebara, whose workers are a thousand times less her weight. She is leaving on her nuptial flight, and a number of workers are clinging to the hairs on her legs.

way, with little knobbed heads. It is these knobs which the ants especially fancy as food, and on which they almost entirely subsist. These underground fungus-gardens are connected with the outer air by ventilating shafts, which are closed or opened to regulate the temperature and the moisture.

When the queens of these agriculturists are preparing to leave the nest on their nuptial flight, they take a good meal of the fungus. A mass of the filaments and of the leaf-mould on which they grow is collected in a little pocket in the floor of the mouth. This pocket is present in all ants, and serves to collect dirt and solid particles out of the food (for no ant ever swallows any food that is not in the liquid state); when the pocket is full the contained pellet is ejected on a rubbish-heap outside the nest. After the agricultural queen is fertilized, she excavates a little earthen chamber, and snaps off her wings. She voids the fungus-pellet on to the floor of the chamber, manures it with her own dung, and keeps the fungus going until the eggs she lays hatch out into grubs; she feeds them with bits of fungus-heads. The grubs pupate and turn into workers. These, all untaught and without a previous glimpse of a leaf, sally out, cut leaves, chop them up, and add to the garden.

Fungi grow readily in the humid atmosphere of an ants' subterranean city. Doubtless these fungus-growers at first supplemented their ordinary diet with a few casual fungi, and only gradually were the instincts evolved which led to the perfection of fungus-agriculture which we see to-day. The transference of the staple vegetable from one nest to another seems at first sight the most difficult evolutionary step; but we see how utilization of the already existing debris-pocket in the mouth, together with a trifling change of behaviour as regards its contents, suffice to bring it about.

The third type that we will choose is that of the grain-collectors. Perhaps we should have put them first because of their literary celebrity. For to this tribe belonged the ants which impressed King Solomon. They have been celebrated in fable from Æsop's day to our own. However,

their achievements, remarkable as they are, are not so extraordinary as those of the cattle-keepers and the fungus-gardeners. It was at one time supposed that these little creatures not only stored grain, but planted and cultivated it. This has now been shown to be a myth. They are in the stage of food-collectors, the stage through which our own forebears must have passed in their transition from hunting to farming. They all inhabit dry countries, and the store of grain is gathered against the season of drought. Sometimes neglected seeds germinate near the nest when the next rains come, and it is this which naturally enough gave rise to the legend of deliberate cultivation.

The soldier-caste of the grain-ants has been partially demilitarized. Their swords have been beaten into ploughshares by evolution—in point of fact, their militarist jaws have been converted into heavy grinding and crushing tools, which are able to achieve what the worker's slighter jaws cannot do—break up the hard grains. In some species the workers then chew up the flour thus produced, moisten it into a paste, and put cakes of it out to bake in the sun. It must, however, be admitted that the soldiers also use their jaws for fighting. Indeed the battles between neighbouring nests for the possession of a store of grain are often very fierce; as in man, stored-up wealth has become an incentive to conquest.

Another remarkable ant of dry regions is the Honeypot, Myrmecocystis. The bees are the only insects which actually make store-chambers for liquid food. But these ants have got over the difficulty by turning some of their own number into living honey-jars. The ordinary workers collect the honey-dew voided by plant-lice; arrived back in the nest, they hand over most of the contents of their crops to a special kind of neuter appropriately called the Replete. These have the capacity of distending their crops until their abdomen swells to the size of a pea, perhaps a hundred times its original bulk. At the close of the wet season the repletes hang themselves up in rows from the roofs of underground cellars, and in the dry season of scarcity they are, so to speak, taken down

and tapped, supplying the whole community for months from their superfluity.

This moulding of the individual's structure so that it becomes a tool of the community is equally well illustrated by the leaf-nest ant, Œcophylla, which inhabits nests made of green leaves glued together. These ants share with man the doubtful honour of being the only known organisms to employ child labour. If you tear a hole in a leaf nest, you will see a gang of workers swarm out and pull the edges of the gap together. Meanwhile, on the inside of the breach, another gang appears, each member of which has a grub in its jaws. When the outside gang have got the leaves in place, the interior workers begin their job. They squeeze the grubs; the grubs exude threads of extremely sticky secretion from their so-called salivary glands, and with these threads the workers repair the damage, dabbing the grubs from one side of the rent to the other. This is child labour, if you will, but with all kinds of fundamental differences from its human counterpart. The children in the mills of Lancashire, three-quarters of a century ago, did not secrete thread like spiders or possess hands like shuttles or carding-combs. But in the ants, the constitution of the grubs has been altered during evolution to fit them for this work. Their salivary glands produce this very adhesive substance, which is different from the secretion of the corresponding glands in ordinary ant-larvæ, and the glands are much larger than usual.

Another remarkable ant variation is the slave-maker. The term *slave-making* is firmly engrained; but in reality the relations of slave-maker to slave are often more like those of parasite to host. The workers of the slave-making species set out and raid the nest of other kinds of ants. The best-known are the Amazon ants, Polyergus. With their long sickle-shaped jaws, they pierce the brains of the defenders, and carry away a store of cocoons. Forel gives some wonderful descriptions of these expeditions, the organization and the tactics involved, the fierce fighting, the occasional repulse of the attackers. The pupæ hatch out in their new

FIGS. 20, 21.—SCENES FROM ANT-LIFE.

(1A) A worker of Polyergus, the Amazon slave-maker, carrying away a cocoon of Formica rufibarbis. One of the Formica workers is trying to retrieve the cocoon. (1B) The Amazon has dropped the cocoon and has pierced the brain of the Formica with her mandibles. (2) A grain-crushing neuter (modified soldier) of Messor, one of the harvesting ants, carrying a seed home in her jaws. (3) A worker of the common field-ant, Formica pratensis, defending the colony. Holding on by her middle pair of legs, she is squirting a jet of formic acid at the enemy. (4) Honey-pot ants. A number of replete neuters, with their abdomens enormously swollen by their crops distended with honey-dew, are hanging from the roof of an underground store-chamber. Below, one of the repletes is regurgitating honey-dew to an ordinary worker.

home, and set about what their instincts impel them to—the care of ant-babies, even though these are not of their own kind; the building of the home, albeit an alien one; the foraging of food. The Amazons themselves do not stir leg or jaw in any such domestic duties—for which, indeed, the build of their mandibles altogether unfits them.

The red slave-maker, *Formica sanguinea*, is not so specialized. Its neuters can still work as well as fight; and old colonies may give up their raids and allow all their slaves to die off. Their queens are unable to found a colony independently; apparently they have not enough reserve materials stored in their bodies. After the nuptial flight the queen either returns to her old home or to another colony of the same species, or else invades a small nest of a related species, the brown ant *Formica fusca*. There she excitedly seizes a number of pupæ and mounts guard over the pile, killing any of the *fusca* workers (who are much smaller than she is) if they try to recapture the cocoons. Sometimes, it seems, the *fusca* queen is killed by the intruder; but sometimes the workers adopt the stranger and turn against their own queen.

The Amazon queen is even more warlike and invariably founds new colonies by invading a small community of the slave species (again usually *Formica fusca*) and killing the queen with one bite of her sickle-shaped jaws through the brain; the *fusca* workers then adopt her and care for her and for the eggs she lays. So the mixed colony of warriors and alien slaves is begun.

This way of life must clearly have arisen out of the general foraging habits of ants. Alien cocoons of some related species, carried away in a raid, aroused the nursing instincts of their captors, and were tended instead of being devoured. The workers that emerged from them would automatically take their place in the life of the colony, which thus would receive an accession of working strength without having incurred the expense of feeding the grubs. And so it would thrive, and any further strengthening of the instinct to raid

and to look after the raided cocoons would be preserved by selection.

The path of biological dependence, however, is a slippery one. In many species dependence has gone so far that the slave-makers are the merest parasites. Ordinary parasites, like the tapeworm, tend to lose their organs of food-finding and of protection against the outer world; they become masses of tissue focused upon food absorption and reproduction. The only department of their life in which there is elaboration above the normal is in their means of dispersal to enable them to make the difficult passage from one host to another. These parasitic ants are no exception. But the biological unit in ant-life is the colony, not the individual, and it is the colony which shows degeneration. In these species the colony has lost all its workers; it has come to consist of nothing but reproductive units, male and female. The queens are found in alien nests, entirely incapable of looking after themselves. Their offspring are the only young ants in the nest. Tended by alien nurses, they grow up into sexual forms, and the fertilized females insinuate themselves into new nests of the host species. The old nest inevitably dies out, for the host workers die of old age one by one, and cannot be replaced.

The crux of the life-cycle is the invasion of fresh hosts. The fertilized queen makes for a nest of the slave or host species, the workers meanwhile looking on without interfering, and then either she herself fights and kills the rightful queen, or the workers even turn against their own queen and kill her. In either case she is then adopted as queen.

This extraordinary behaviour of the host workers, who do not treat the alien as an intruder, but accept her and passively or actively turn against their own flesh and blood, is one of the strangest facts of biology. It is as if a human community adopted and worshipped a royal family of aliens. It seems to depend on the alien queen having been furnished by natural selection with a bribe. Since the time of Solomon, ants have been held up as moral exemplars; but, as we shall

see in our next section, they have their weakness—greed. These parasitic queens have their bodies beset with glands which produce a rather fatty, sweet-smelling and sweet-tasting secretion; and the host-workers can be seen licking this with the greatest avidity off the tufts of hair on to which it exudes.

§ 6

The Parasites of Ant-colonies

The individual ant has its own internal parasites; but the ant-colony, that amorphous beginning of a new and compound individuality, is the real unit of the species and harbours many more hangers-on. Already over 2,000 species of animals, mostly insects, but with a fair sprinkling of spiders and mites and a few crustacea, have been discovered living in the nests of ants, and incapable of existing anywhere else. That is about half as many kinds of colony-parasites as of ants.

In this respect, the communities of ants and termites have attained a complication beyond that of human societies. The relations of the ants to these ant-guests, indeed, are very different from those between man and his domestic animals and pets. Ants have no other domestic animals but aphids and scale-insects. These are their milch cattle; but they have no beasts of burden like horses or camels, no animals yielding them clothing like sheep or vicuna, none whose eggs they take, like poultry, or whose flesh they eat like ox or pig, no companion and guard like the dog, no vermin-catcher like the cat. Nor do they have any pets deliberately domesticated, like canary or goldfish or fancy mice, for their attractiveness.

For in the insect-world the whole mechanism by which things happen is different. The guests and parasites of the ant-colony have been moulded to their present queerness of structure and behaviour by natural selection, not by artificial selection. No conscious purpose on the part of the ants

themselves has intervened in their making. As we shall see, the tastes and habits of the ants themselves have contributed to the evolutionary shaping of the guests' germ-plasm. But the shaping has been always indirect; the ants are part of the guests' environment, and if the guests are to survive, they must be adapted to life among ants as tapeworms have had to become adapted to life in vertebrates' intestines. Some of the smaller hangers-on of humanity, like the cricket on the hearth or the house-martin, have become adapted in this way to their human environment; but all such creatures are very small compared with man, while ant guests, almost without exception, are about of a size with their hosts.

If we imagined that in England our houses were, against our wills, inhabited by cockroaches as big as wolves and house-flies like hens, and that there were also crickets to whose presence we were indifferent, although they were the size of our own children, and pet-like creatures whom we liked because they rendered us some agreeable service, as it might be parrots which had the instinct of scratching our backs for us; and monstrous animals which we allowed to eat our babies in their cots because they secreted hot rum-punch or some equally fascinating liquid, and that in France, say, and the United States, there were similar sets of animals, willy-nilly sharing men's houses and reproducing there, only all belonging to different species from those of England; and finally that they were all incapable of existing permanently anywhere outside our houses; then we should begin to get some idea of the ants' menagerie of guest-animals.

The simplest relation between a colony-parasite and host is one of simple thieving on the part of the parasite, unmitigated hostility on the part of the ants. One of the most amusing and impudent of such thieves is Lepismina, a wingless silver-fish insect. When one of the worker-ants is engaged in regurgitating a drop of food to a sister, Lepismina steals up, crawls below their upraised bodies, makes a sudden snap at the drop of liquid as it passes, and bolts. Regurgitation is a ticklish matter, and demands rather a

FIGS. 22-26.—SOME GUESTS AND PARASITES OF ANT-COLONIES.

(1) A beetle, Mimeciton, which closely mimics the Driver-ants with which it lives. (2) The beetle Atemeles soliciting a worker Myrmica to regurgitate food for it by caressing the ant with its fore-legs. In return it will allow the ant to suck the secretion from the tufts of yellow hairs on its abdomen. (3) The silver-fish Atelura rushing up to snatch the drop of liquid food that one Lasius worker is regurgitating to a second. (4) Another Lasius worker which is carrying three mites, Antennophorus, one under its head and one on either side of its abdomen. (5) A Honeypot worker with two little beetles (Oxysoma) attending to its toilet.

delicate pose on the part of the two ants engaged upon it. Before the aggrieved couple can disengage themselves for pursuit, the thief is generally well away towards safety. But Lepismina has always to keep out of its hosts' way if it does not want to be attacked and killed. There are some parasites, however, of which the ants take no notice. The maggot of the little fly Metopina, for example, is found in the nests of an ant called Pachycondyla, clinging round the necks of the ant-grubs. In these ants, the grubs are fed by a primitive method; pieces of insect-meat are placed in a natural trough which the grub grows near its mouth. When food is given to a grub round whose neck a Metopina is wrapped like a boa, the parasite uncoils, helps itself, and coils up again. The ant-nurses pay no attention to it at all; they clean it as if it were a part of the ant-grub. Apparently it has acquired the authentic nest-smell, and this is enough to make the nurses overlook the very abnormal shape of those of their charges which are being exploited. Then there are other parasites which, though the ants are perfectly aware of their presence, are tolerated. One of the queerest of these is the mite, Antennophorus, which rides about on the heads and bodies of its host. Although it is as big in comparison with its host as a small monkey in comparison with a man, up to four or even six may be found on a single ant. To secure food, these creatures employ a trick found in many ant-guests; they stroke their hosts so as to simulate the food-begging caresses of one worker soliciting another to regurgitate. And they get what they ask for. In all ant-guests which solicit food by stroking, the organs for soliciting and caressing are moulded into passable imitations of ants' antennæ. Sometimes these caressing organs are the parasites' own antennæ; but often, as in Antennophorus, one pair of legs is made antenna-like. It is as if a badger or a squirrel were to grow imitation human lips on the end of his tail to kiss us into giving him his dinner.

Still other parasites are fed for services rendered. One little beetle, for instance, called Oxysoma, seems to perform

various agreeable toilet duties for its hosts, licking them clean and pleasantly stroking them.

Finally come the strangest gang of all—those parasites of the colony which are not only tolerated, not only paid with food, but looked after and protected by their hosts, sometimes before the ants' own flesh and blood. And the reason for this unnatural behaviour is the ants' boundless greed. The parasite exploits the cravings of its hosts by offering them a delicious secretion to lick. Worker-ants and termites thus share with man the unenviable distinction of being the only animals with vices.

Most of these vice-exploiting parasites, these perambulating bars of the ant-world, are beetles. There are several hundred species of them; they all produce the special sticky secretion which their hosts like so much, and this always oozes out on to bunches of special hairs, which act as teats from which the ants can suck the juice. The beetles usually have had their antennæ altered so that they are like ants' antennæ. Thus the beetles earn a living by providing luxuries in return for necessities. Their relation with their hosts is a perversion of the normal food-exchange on which the life of the ant-colony is based. The ants, like many human beings, put luxuries first; at a threat of danger, the beetles are generally carried off to safety before the ants' own grubs and pupæ.

The most remarkable of all guest-beetles is Lomechusa, a parasite of the Red Slave-maker, *Formica rufa*, whose history has been unravelled by the Jesuit entomologist, Wasmann. Not only does the adult beetle live by pandering to the ants' gustatory desires, but its grubs appear to exude some equally desirable bribe. The ants look after the beetle-grubs better than their own brood, and even allow them to eat the ant-grubs. As a result of the neglect of their beetle-infatuated nurses, a large proportion of the ant-larvæ perish; others are wrongly dieted and grow up as useless intermediates between workers and queens. A heavily-infected colony of the Red Slave-maker is doomed to extinction; but such

heavily-infected colonies are rare, and the parasite itself sporadic and infrequent.

This perversion of the normal nursing instincts of the workers argues overpowering attractions in the beetles' secretions, comparable to those possessed for human beings by spirits or opium. But there is always some striking difference between insect and man. There are human beings who neglect their children for drink; but the behaviour of the ants is as if a mother were to abandon her baby for the charms of gin or brandy-butter which she lapped off as it exuded from the body of a changeling creature. Professor Wheeler, in his *Social Life Among the Insects*, admirably sums up the situation:

> Any insect possessed of these glandular attractions . . . can induce the ants to adopt, feed and care for it, and thus become a member of the colony, just as an attractive and well-behaved foreigner can secure naturalization and nourishment in any human community. But the procedure among the ants is more striking, because the foreigners are so very foreign. . . . Were we to behave in an analogous manner we should live in a truly Alice-in-Wonderland society. We should delight in keeping porcupines, alligators, lobsters, etc., in our homes, insist on their sitting down to table with us, and (in some cases) feed them so solicitously that our children would either perish of neglect or grow up as hopeless rachitics.

§ 7

Termites

Termites and ants afford a wonderful example of parallel evolution. Termites, though sprung from a stock related to the cockroaches and differing fundamentally from ants in having no grub-stage and no metamorphosis, but hatching from the egg as babies of the same general build as their parents, have evolved independently a social life strikingly similar to that of ants. They, too, have sexual and neuter castes; the neuters are often divided into workers and soldiers; their cities are an irregular network of galleries and chambers; the community's economic existence is based

on an elaborate system of food-exchange; they have numerous colony-parasites, many of which exploit their hosts' greed just as do the guest-beetles of ants' nests; and some species even cultivate fungi in a way almost identical with that of the fungus-gardeners among ants.

But when we look into the organization of the termite state, we find interesting differences of detail between it and the ant community. The neuters are not all neuter females; there are neuter males as well, in equal abundance with their sterile sisters. Then when we find soldiers in addition to workers in a colony, the two castes are not merely unlike in their bodily proportions, as with ants, but qualitatively unlike. This and other evidence has led many biologists to believe that the differences between sexual individual, worker and soldier, in termites, are not an affair of feeding, as with ants, but are due to some elaborate hereditary machinery, such as that which controls the production of the two sexes in most higher animals. There is a further probability in this: since the young, growing termites are free to feed where they will (in the gardener termites the young have been described as browsing like miniature white lambs on fungoid herbage of equal whiteness), it is difficult to see how their diet could be regulated. But full proof is as yet lacking.

Then not only are there neuter males, but the royal, sexual males help in founding the colony, unlike the male ant, whose services to the race are at an end with his single act of fertilization. The kings and queens, as in ants, fly out into the world when the time comes to mate; however, their flight itself is not a nuptial flight, but an opportunity for the young people to meet. A male and female join fortunes, descend to earth, both shed their wings, both set to and excavate a nest, and only then is the marriage consummated. The fully fertile queen usually grows to an unbelievable size, several inches long, her original slimness revealed by the patches of dark chitin which once made a continuous skeleton, but now are separated by areas of white egg-distended skin.

Some of these queens lay eggs almost continuously, at the rate of about one egg every two to four seconds, for many years.

Besides these fully developed queens there may be numerous "second form" and "third form" females, which possess reproductive organs, but are in other ways intermediate between the true queens and the wingless workers; these always remain unbloated. And there may be a similar gradation in the males. The function of these creatures in the colony is obscure; we know, however, that in some species, instead of soldiers, there is a special caste of neuters, the *nasuti*, or "nosy ones," who constitute a sort of chemical warfare corps. These have long snouts on which open the ducts of special glands that secrete an unpleasant liquid which is extremely sticky, and possibly corrosive as well. With this the nasuti immobilize their enemies by gumming them up—legs, antennæ, and body—in a helpless mass. The size of these defence glands in some of these creatures is enormous, much bigger than all the other organs put together—a visible proof of the extraordinary degree to which division of labour has specialized the various castes.

One of the most curious and uncanny things about termites is the fact that all of them, save the winged sexual kings and queens, are subterranean creatures that shun the light. The workers forage for hundreds of yards round the nest, but always at night or else under cover of tunnels which they build for themselves as they go. When they reach a supply of food, whether it be a log in the forest or a piece of human furniture, they eat it out from the inside. Finally it becomes a mere shell and collapses at a touch. The workers are all pigmentless, fleshy, white creatures; the winged kings and queens, which will one day have to brave the light, are dark brown. The soldiers have huge, cast-iron heads, but soft and defenceless bodies; the hard heads are brown, the soft bodies white.

Parallel with this shunning of all direct contact with light and the outer world by termites has gone a specialization of

their nests. Only in the more primitive termites do we find diffuse nests, underground or in dead wood, like those of most ants. In tropical forests there are many tree-nests, usually made like wasps' nests of chewed-up wood cemented by saliva. Some are as big as a good-sized barrel; others are plastered on to trunks like a cluster of sausages and are protected from rain by a series of inverted carton V's built above them.

Tropical ants build tree-nests, too; but no ants have nests resembling those of some African termites—stalked objects protruding from the ground with a mushroom-like top acting as an *en tout cas* against both rain and sun. The highest developments of termite architecture are the giant termitaries (wrongly styled "ants' nests") of African and Australian tropical scrublands, which may harbour over a million individuals, reach a height of fifteen or twenty feet, and are so concrete-like in their strength and hardness as to be almost indestructible save with the aid of dynamite. In some parts of Africa the abundance of these nests makes the clearing of aerodromes a costly and laborious business.

It is in their food-economics that the termites are most extraordinary. In the first place, they live almost exclusively upon wood. This is entirely indigestible by most animals, so that the termites here enjoy a notable advantage in the struggle for existence. But they are only enabled to do this by means of a remarkable partnership with another kind of animal. In their intestines live swarms of microscopic single-celled flagellates, and it is these which have the capacity for digesting wood. The termite workers find and eat the wood, the flagellates make it available, and both parties live on the products.

Maeterlinck, in his book on termites, holds up the termites' capacity to digest wood and the presence of neuter castes in their societies as proof of more than human intelligence. This is uncritical fantasy. The two types of existence stand on a different level. The termites, we can be completely certain, do not even know that they possess flagellates in

their insides, or that these digest wood for them; and even if they did know, the presence of these admirable aids to digestion would be no more due to cleverness on the part of the termites than is the presence in our insides of that remarkable fluid, the pancreatic juice, due to our cleverness. And similarly with the castes. Workers and soldiers are what they are because natural selection has moulded the

FIG. 27.—THE RAVAGES OF TERMITES.
A piece of wood excavated by white ants at Singapore.
(*Courtesy of the British Museum, Natural History.*)

termite germ-plasm in a particular way, not because of any forethought or conscious planning by the insects themselves.

Only the workers and soldiers contain the precious flagellates, because only they eat wood. The rest of the colony receive their food from these wood-eaters. The details of their food exchanges we have already mentioned. Even their concern for their precious, swollen-bellied queen

is in return for food. Hundreds of workers are generally to be seen in attendance upon the queen. It used to be supposed that they were actuated by the motives which prompt human worshippers. But once more the gulf between man and insect is revealed. They surround the queen because she exudes a specially rich and fatty secretion; and their apparent attentions consist in licking her to get something for themselves—sometimes so violently that they rasp holes in the royal side.

Termites do not spread so far out of the tropics as do ants, but where they are abundant they are of more economic importance. They are extremely destructive, not only to wooden fences and buildings and furniture, but to paper. And since ink and the written or printed word are no deterrents to their hunger, books and documents are continually being destroyed by them. Von Humboldt noted that in tropical South America books more than forty or fifty years old were great rarities; before attaining such an age they generally went to feed termites. Some authorities, indeed, believe that the termites' destruction of books is one of the chief reasons which have hitherto prevented tropical civilizations from reaching any pitch of progress comparable with that of more temperate nations. Our descendants will be able to judge whether this suggestion is true or no, for some tropical countries are now constructing libraries and archives with concrete foundations to make them termite-proof.

On the other side of the account must be entered the fact that termites (unlike ants) are beneficial to plant growth. Cellulose and wood are among the most resistant of organic substances. The termites, in combination with their indispensable flagellate allies, are among the few agencies which rapidly break them down. And thus much of the capital of life, which would otherwise be locked up for years, is speedily brought back by termites into the vital circulation.

§ 8

Bees

In ants all stages in the evolution of communal life have been lost, but in bees there survive many stages in the process. There are bees which are entirely solitary, where the females simply store up food for their grubs and leave them to hatch out untended. There is here no trace of social life, and yet it is the first step towards it, since the social life of insects has evolved in connection with the care of the young. A further step is seen in bees like Halictus, where the female stays by her little nest and waits until her children emerge as winged creatures as big as herself. The children then add to the nest and throughout the summer there is a true colony-life. But autumn breaks up the community, and the females that survive the winter must each found a separate nest again. Here is no continuity of social life, nor is there any division of labour between castes.

The humble-bees illustrate the next step. The community still endures for one season only, but it shows the beginnings of a worker-caste. The females that were fertilized in the previous autumn and have successfully survived hibernation, dig themselves an underground chamber in which they build a few irregular rounded cells. In the first cell they lay perhaps half a dozen eggs, put up with them a supply of honey and pollen, and seal the cell up. From time to time they open it again and give the grubs fresh food. But the solitary mother can only manage to provide the bare minimum of food, and the weight of the bees that hatch out is only some fifteen or twenty per cent. of their parent's. Further, the machinery of humble-bee development is so arranged that the ovaries only grow properly when food is abundant. Accordingly these first stunted bees have rudimentary ovaries, and are sterile; they are in fact neuter workers. They help their parent in the duties of the nest; with their aid, food becomes more abundant, the state's new

children bigger. As the season goes on, all transitions are thus produced between sterile worker-females and fertile queen-females; and by late summer queens are plentiful. Males are also produced in late summer; and though they do not help at home, they at least support themselves by gathering their own food; they are thus not so specialized as the males of ants or hive-bees, which have become merely male reproductive organs for the colony, nourished by the efforts of its other members. Winter kills off all the males and workers, since the reserves of food are but scanty.

In several ways the characteristic features of the hive-bees' advanced polity are foreshadowed in a half-and-half condition by the humble-bees. They possess neuter workers; but these differ from the queens only in their sterility and their size, not in their construction and instincts. The queens still undertake other duties than that of a mere egg-laying machine, the males do not deserve the name of drones, for they still feed themselves. The females, like worker hive-bees, secrete wax, sweating out plates of it from between the crevices of their chitinous armour; but wax is not yet used as sole building material, being mixed with resin and pollen before use. The humble-bee does store up food; some of the empty cells from which workers have hatched out are used as honey-pots. But they build no special combs of cells all devoted to honey-storage, and the amount of stored food is small.

In other bees, further gradations to the fullness of social life are to be found; but we will pass straight to the consideration of the most specialized of bees and the only insect to have been domesticated by man, the hive-bee.

The bee-hive, like the ant-nest, is on the way to become a super-individual. It has the same division of labour; the workers work for the community, the queen lays eggs for it, the males are sacrificed in autumn for its good. It is in certain ways more of a unit than the ant-nest—it has one queen, not many. It shows its incipient individuality in another interesting way. Although its separate members

cannot maintain a constant temperature, the community can and does. The bee-hive, at least in winter and spring, is for most purposes a warm-blooded organism. In winter, if the temperature falls too low, the bees set the heating machinery in motion. They assemble hanging from the roof in a dense bunch; when this cools to a temperature of about 55° F., the bees get restless, they take a meal of honey, come back and crawl actively within the cluster. The heat produced by their movements cannot readily escape from the dense mass of bodies; and the temperature rises rapidly —within an hour it may jump from 55° to 75°. The outer bees make the skin of the cluster cool off first; then they crawl into the interior and others take their place, until finally the whole cluster is cooled to 55° again. This takes the best part of twenty-four hours; and then the heating process is repeated.

In spring and summer, however, when the development of the young brood is going on, the hive becomes fully "warm-blooded"; the bees keep it almost at blood-heat (actually 93° to 95° F.), whatever the outer temperature. At lower temperatures, the grubs not only develop more slowly, but abnormally; and temperatures much higher than this would be as fatal to bee-protoplasm as to our own. On cold days the workers who are looking after the brood crouch and crawl in a thick layer over the brood-cells, so constituting both a protection against heat-loss and a source of warmth. On hot days they fan their wings, drawing cool air through the hive.

It is often asked how any theory of inheritance can explain the facts of bee-life. The workers alone have the elaborate instincts which keep the business of the hive going; and yet they leave no descendants. The drones do nothing but fertilize the queens, the queens nothing but lay eggs; and yet they give rise to the gifted and industrious workers. The same question, of course, applies also to ants and termites. The question would perhaps not be asked if it were not for the unconsciously held Lamarckian beliefs about

heredity which most people cherish: they are surprised that the workers can do things which none of their ancestors ever did. The difficulty is not so great as it seems; it disappears as soon as we think in terms of the modern idea of the germ-plasm. The case of worker-bees is precisely the same as the case of specialized tissues within our own bodies. Our muscle-cells, our blood or glands, our brain-tissues – none of these leave any descendants: they do their jobs in our economy in spite of the fact that they are descended from a long line of germ-cells which have never done anything of the sort, but have merely divided, become gametes, fertilized one another, and divided again. So with bees. The queens and drones are the germ-plasm of the community, they alone are part of the immortal racial stream; the workers are its body or soma, doomed to work and die for it without direct posterity. As the same human chromosomes in two different parts of the embryonic environment will set to and help build up tissues as different as muscle and nerve, so the same bee-constitution with one kind of diet will generate egg-laying queens, with another busy neuters.

The instincts of the workers can be kept up to the mark by natural selection. Those fertile females whose genes under worker-diet do not develop into workers with proper instincts, will produce inefficient hives; such communities will go under in the struggle for existence, and so the defective genes will be eliminated from the bee germ-plasm. Here again the process is analogous to what happens in our own bodies. Those germ-cells whose genes give rise to inefficient thyroids or brain-cells will be eliminated from the race, although as mere germ-cells they may be adequate enough. Once more we see the community as the true unit of the bee or ant species, the single bee or ant as a subordinate member of this super-individuality.

There are numerous books, both scientific and popular, on the hive-bee. To them we must refer the reader for the picturesque details with which bee-life abounds. Here some

interesting and very recent work of the Bavarian zoologist von Frisch must suffice. His patience and skill have elicited many new facts, and have set many old ones in a new light.

The essence of this method has been intensive observation of individual bees leading their natural life. As there may be thousands of bees in a hive, and as they all look alike even to a trained eye, the first requisite was some means of identifying individual workers. To this end von Frisch modified and improved the marking method which Lord Avebury was the first to use. He caught bees, and by means of combinations of dabs of bright colour on different parts of the body, gave them labels which made identification easy, even in flight. If a white spot on the thorax is taken to mean 1, the same colour on the abdomen to mean 6, red on thorax is 2, on abdomen 7, and so on, a glance at a marked bee enables you to write down its number. With the aid of this method, of specially-devised observation hives, and of infinite patience, von Frisch discovered how the numerous duties demanded of the workers—nectar-gathering, grub-feeding, comb-building, and the rest—were distributed. The reception of such paint-marked bees by their fellow-workers is worth noting, as it throws an interesting side-light on bee-mind. No difficulty is made about old bees; but ones that are taken and painted immediately after emergence are roughly handled and usually thrown out of the hive or stung to death. The unfamiliar smell of the paint is reacted against unless the familiar nest-smell is superimposed. But if the young bee is smeared with a little honey as well as being painted, the honey is licked off, and after this she is accepted without more ado.

In human communities, division of labour comes about by different people learning to do different kinds of work. You are not born a lawyer or a colonel; training and experience are needed. In the more specialized kinds of ants and termites everything, or almost everything, depends on heredity; different jobs are performed by creatures who are born different—soldiers, workers, and so forth. But

in bees a third method is adopted. Queens, males, and workers are born different; but the workers' instincts develop and change with time so that they take on different jobs as they grow up—as if human beings should automatically and without training change from nurse-maids into bricklayers, then into hall-porters, and wind up in business.

A queen-bee may live five years; but workers die of old age after about five weeks of winged existence. (To this must be added three weeks' development—three days as an egg, six days as a growing grub, and twelve days as a resting pupa.) This short span of adult life falls into three main periods. The first, which the bee spends entirely inside the dark hive, guided by smell and touch and hardly ever employing her eyes, lasts about ten days and is concerned with the care of the young. The second, from about the tenth to the twentieth day, is concerned with building, cleaning, and acting as guard at the main gate of the hive, with occasional short excursions. And the third, from three weeks old till death, is spent mainly outside the hive, and is concerned entirely with collecting pollen and nectar.

We may follow an individual bee through her life-cycle in a little more detail. On emergence from her pupa-skin and cocoon, she gnaws open the thin wax lid of her cell, which was sealed over her when she had ceased to grow and had turned into a pupa. Then she dries and cleans herself, and within an hour, all uninstructed, may have begun work. She begins cleaning out cells from which other bees have hatched, removing debris and licking their walls with her saliva. Only when cells have been thus treated will the queen lay new eggs in them.

But in the first three days the young bee sits about a good deal doing nothing in particular (the idea that bees are always busy is a delusion, which springs from the fact that we notice them at work, not when they are resting; to someone stationed in a central street of a great city, it would appear that human beings were always busy). Apart from cell-

cleaning, the only other duty of the young bee is keeping the brood warm on cold days by blanketing it with its body.

When the young worker is about three days old, however, the nursing instinct stirs within her, and she begins feeding the older grubs with honey and pollen from the communal stores. The younger grubs, however, cannot digest raw pollen, and have to get their nitrogenous food from a secretion made in the worker's "salivary" glands. This is closely parallel with the feeding of the human infant on milk, and is one of the few cases of an invertebrate animal feeding its young on specially-secreted fluids. On about the sixth day of a worker's life, these glands suddenly begin to swell and grow, just as the milk glands in the breasts of a woman grow in preparation for suckling her child. With the growth of the glands, there develops the instinct to use them; and from about the sixth to the tenth day the worker does little but nurse the young grubs. Then the nurse-glands shrink again, and the bee's impulses prompt her to new activities. She takes nectar from the older bees returning from their work among the flowers, and pumps it into honey-cells; packs the pollen tight in the pollen-cells; and removes dirt and debris a short distance outside the hive. In place of the shrunken salivary glands, her wax-glands have enlarged and sheets of wax grow out and protrude between the plates of her abdomen. With this, her building instincts come into play, and she spends a good deal of time on the construction of new comb. Besides the ordinary cells which may serve either for honey, pollen, or developing brood, workers of this age may build cells of the same shape, but larger, whose greater dimensions stimulate the queen, as she pokes her abdomen into the cell, to lay an unfertilized instead of a fertilized egg; these are the drone cells, since unfertilized eggs grow into males. If the workers decide to bring up a female grub as a queen, they build a protruding and very large "queen-cell."

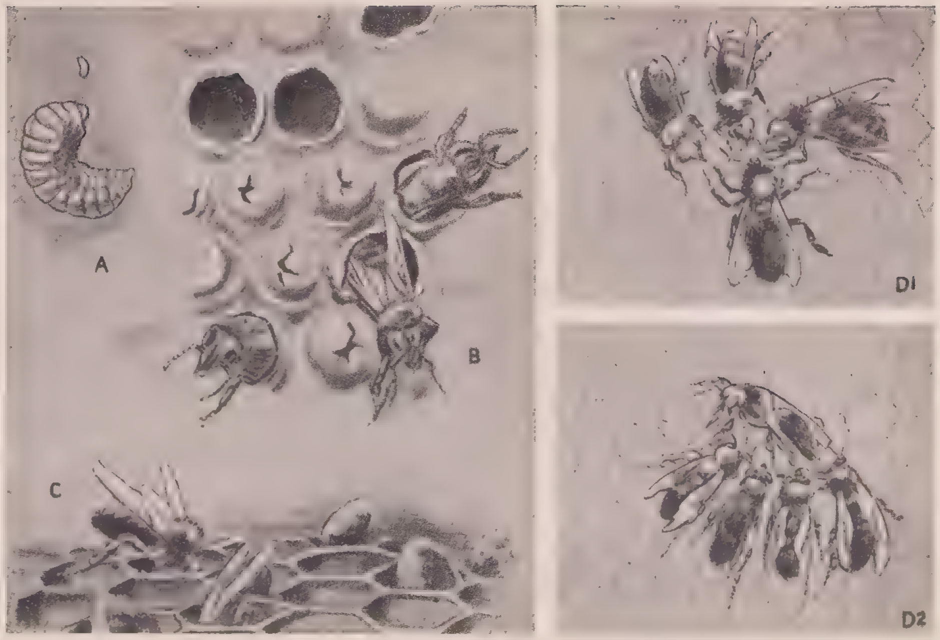
All through this period, the workers, prompted by a new restlessness, will occasionally leave the hive and take short

flights to get to know the surroundings. These explorations are pushed farther and farther afield, until before she is three weeks old, a worker has a good knowledge of all the neighbourhood within a few hundred yards.

Before she goes off collecting from flowers, however, she spends two or three days on guard-duty—work that is on the dividing line between her previous life inside the hive and her future activities outside it. There are always a few guards or door-keepers near the entrance to a hive, some just within it, some just outside, and these are always eighteen to twenty days old ; so accurately do the different instincts succeed each other in a worker's life. They investigate the entering bees with their antennæ, and will drive off any members of a strange hive. They attack marauding wasps or other creatures who try to gain entrance to make free with the community's honey-stores, and it is they who will fly out and sting big animals or human beings who carelessly approach the hive.

It is a well-known fact that if a bee stings a man, the sting sticks in his skin and is torn out, and the bee dies. But this does not happen when a bee attacks a creature its own size ; the deadly sting (which is an ovipositor or egg-laying tube converted into a weapon, with certain of the attached glands made over into poison-secreting organs) can be used over and over again on another insect. This particular sacrifice of the worker in the interests of the community is only demanded on the rare occasions when large animals are to be stung.

Only after about her twentieth day does the worker begin food-gathering. All her work is now to visit flowers, suck up nectar, and collect pollen. The nectar she brings back in her crop or honey-stomach, vomiting the contents up again on her return, either into store, or usually to other younger workers, who themselves either feed others or pump the nectar into cells. Her honey-stomach is about the size of a pin's head ; she must fill and empty it over fifty times to get a thimbleful of honey. And it takes the contents of



FIGS. 28, 29, 30.—SCENES FROM THE LIFE OF THE HONEY-BEE.

(A) A bee's egg and a full-grown grub on the same scale. (B) Worker-bees emerging from their cells. Some cells are unopened; others are just being gnawed open; from others bees are emerging. (C) The workers' first duty: cleaning out cells for the queen to lay eggs in. (D1) A bee returned from honey-gathering regurgitating food to three other workers. (D2) Before flying off again she executes a dance over the comb, followed by other workers, who smell her with their antennæ.

over a thousand clover flowers to fill it once! When we remember that a single hive may store over two pounds of honey in a day, in addition to what it eats, we begin to realize the efficiency of the bee as a device, evolved late in the history of life, for exploiting the secretions of flowers.

On cold, rainy days, the food-gatherers do not go out much, but sit about on the combs (thus unconsciously helping to keep up the hive's temperature). Eventually they grow old, and spend much time doing nothing, even on fine days; and at last, if they have met with no accident, they die of old age, and their corpses are transported out of the hive by their sisters, and thrown away.

The most novel and interesting of von Frisch's discoveries concerns what has been sometimes called the language of bees. It is so far a language in that it is a means of communication, that by its aid they convey information to each other about the available sources of honey and pollen. But, as always, there is a radical difference between insect and human methods. The so-called bee-language is really only a chain of stimuli. It is based on a strange and elaborate system of instinctive or reflex actions, not learnt by a painful process of associating symbols with meanings as ours is, and the result, though effective for its purpose, is achieved without the aid of any powers deserving to be called intellectual.

Before the experiments on this means of communication could be planned, it was necessary to find out a good deal about the senses of bees. It was shown that bees' eyes, like our own, distinguish colour. But they do not distinguish it in quite the same way as we. For one thing, they see farther up into the ultra-violet than we do, but are quite blind to most of the wavelengths which to us appear red. (That is why flowers visited by bees are very rarely pure red.) For another, though they distinguish between different intensities of illumination, different grades of black, grey and white, as well as we do, their discrimination of colour-shades is a good deal less accurate. They distinguish readily enough between the whole group of colours included be-

tween blue and violet and the other whole group between orange-yellow and yellowish-green ; but they cannot see any difference between the tints within each group –yellowish-green and orange are alike to their eyes. They can also distinguish one form from another, but not so thoroughly as we ; interestingly enough, objects whose shapes recall the shapes of simple flowers are more readily learnt and remembered. They see quite well, but a good deal less well than birds or men.

Bees, again like other insects, have their sense of smell, as well as their most sensitive faculty of touch, in their antennæ ; and experiment shows that they can distinguish various smells readily enough. Once bees have been taught to associate the smell of peppermint, for instance, with a supply of sugar-water, a drop of peppermint oil will attract them from a considerable distance. On the other hand, bees are only about as sensitive to smell as men, and fall far below dogs or certain moths in their olfactory capacities. They are even excelled by the professional perfume-experts employed at scent-factories when it comes to distinguishing between two very similar smells.

They have a brain-machinery which enables them to use these senses in quite a varied and effective way. They can be trained to associate particular colours and forms and smells with food, and to remember the association apparently for the rest of their short lives. By pretty experiments it has been shown that when both colour and scent have been associated with food, it is the colour which they look for and recognize while still at a distance, while the effect of the scent preponderates when they are close. If, for instance, they have been used to find food inside a small box painted yellow and scented with oil of roses, and then a number of similar boxes are set out, one unscented but painted yellow, another not painted but smelling of roses, they will begin by flying straight to the yellow box, but will check and refuse to enter it when they miss the familiar scent ; however, any which then happen to come within range of the

smell of roses will enter the scented box, though it lacks the familiar yellow colour. As we shall see later, this is what happens in nature; different flowers are recognized far off by vision; but smell is the final means of identification.

The bees' powers of finding their way are remarkable. If you catch a bee as it is entering the hive, imprison it in a box, mark it with a dab of colour, and liberate it a mile away, in a few minutes it will be at the hive again. Some observers have thought that bees and other insects possessed a special "sense of orientation" through which in some unexplained way they were drawn back to the hive, but this is a baseless and needless assumption. The bee learns the lie of the land round the hive by exploration flights. The flights grow longer and longer, until a radius of two or three miles is thus learnt by heart; but if you take your captive bee beyond this radius, she is hopelessly lost.

Even when there are a number of similar hives in a row. the bees usually find their way back to the right hive. But mistakes are by no means infrequent, as you can convince yourself by marking a series of bees from one hive. Indeed, we should expect mistakes, for finding the right hive must be as hard as finding the right door in a long, drab street where the houses had no numbers. When a queen makes a mistake on her return from her marriage-flight the matter becomes serious; for she will get killed in a strange hive, and her own hive will be queenless and will peter out unless the workers manage to raise a substitute-queen. Accordingly, for years past, many bee-keepers have painted their hives different colours; but opinions were long divided over the value of this measure. The discovery of the limitations to bees' colour-vision has cleared everything up. Colours do help the bees to find their way home—but, naturally enough, only if the bees can see them. Black, white, yellow, grey, blue—the bees can and do profit if these colours are used to identify their separate hives; but if you put bright-yellow next to yellowish green or orange, or blue next to purple or violet, or red next to dark grey, it is no help to

them, because to their eyes those colours look alike. Von Frisch records that in 1922 the monks of the Bavarian monastery of St. Ottilie, who have a very large apiary, began to paint their hives in accordance with these biological discoveries. In the two previous years, sixteen out of twenty-one young queens had been lost; in the next five years only three out of forty-two.

In the absence of colour-differences, the bees go by differences of shape and by surrounding landmarks, big and small. In addition, smell is employed to help. Bees have a special scent-organ near the hind end of their bodies; and it has been shown that the bees of different hives exhale scents which their sense of smell can distinguish. As with ants, home and patriotism are linked with smell. A number of workers may often be seen near the entrance of the hive, using these organs to dab their special scent on the alighting platform, and then fanning with their wings, so as to drive the scented air out as a recognition-mark for their compatriots. And this is done especially in early spring, when memory is dim after the winter, or a swarm has started life in a new situation, when the landscape is still unfamiliar.

Two other remarkable faculties help the bees to find their way home. One is their power of guiding their flight by the direction of the sun. If, on a sunny day, you imprison a bee while it is feeding, and then liberate it after two, four or six hours, it will at once start off on a straight course, as if it knew the way for home; but the path it chooses is not the right one; it makes an angle with the right direction, and that angle is precisely the angle through which the sun has moved in the intervening time. This curious faculty of steering by the sun is not uncommon in insects; ants in particular, since they cannot fly, have to rely on it to a great extent.

We can thus prophesy the direction-line a temporarily-imprisoned bee will take on liberation. If we mark her, and post observers along this line, we discover a further remarkable fact. She does not simply go on and on in this direc-

tion; when she has covered a distance about equal to that between the point where she was captured and the hive, she ceases her straight flight and begins questing around in bigger and bigger circles until, if she is lucky, she finds the hive. The distance which she traversed on her outward flight is in some way recorded in her brain. This faculty of automatically recording distance (which probably depends in a bee on the number of the wing-beats she has made) is possessed by many animals, vertebrates as well as insects; not only is it prominent in ants, but when rats learn to run a maze, it is this on which they largely rely.

The bees' dependence on this "compass sense" and "sense of distance" can be dramatically demonstrated by imprisoning a feeding bee, at once walking with it to a spot some way on the other side of the hive, and setting it free. Guided by the sun, it now flies directly away from the hive; but stops and searches when it has flown the right distance. Bees in nature use any and every one of these methods of finding the way home—sight, smell, compass-sense, and sense of distance; the emphasis falls on one or the other according to the nature of the country round the hive.

With this knowledge about the capacities of their senses and their memory, von Frisch could go on to the real kernel of his experiments. If you put out a source of food—a strip of paper smeared with honey, or (better for experimental purposes) a little dish of sugar-water—not too far from a hive, sooner or later it will be discovered. It is almost always some hours, and often several days, before this happens; but once one single worker has found it you can be sure that within the next hour or two it will be visited by scores or hundreds of bees. Somehow the hive has been told.

Marking, watching, and waiting enabled von Frisch to unravel the story. A bee that has found a new source of food flies back when her crop is full. In the hive she pumps up the shining drop of liquid and gives it to younger workers. Once rid of her burden, she begins a peculiar little dance,

running with rapid steps in narrow circles over the comb, first in one direction, then in another (Fig. 30). The dance, which always takes place in a crowded part of the hive, creates a good deal of excitement among the bees near the performer. They run after her, trying to touch her abdomen with their feelers. After anything from a few seconds to a minute of this excited dance, with its comet-tail of interested bees, the dancer stops. She may repeat the dance somewhere else, but soon goes off again to fetch more nectar, repeating the performance each time she returns with a full load.

It is easy to convince yourself that the dancer does not act as a guide when other bees follow to the source of food; and yet in a short time there will be plenty there. It looks as if the bees must have a real language, and that the dancer can tell her fellows that there is a good bed of clover under the hedge 200 yards south-south-east, or a dish of sugar-water in the angle of the garden wall—information which they then act upon at their leisure.

Experiment dispels such illusions. If you provide a dish of sugar-water, mark the first few bees that visit it, and then put out half a dozen more dishes in different directions and at various distances from the hive, then although all the marked bees return only to the original dish, within an hour all the dishes will have been discovered by unmarked bees. The dance is simply a sign that food has been found; it stimulates honey-gatherers who have been sitting quiet at home, and impels them to go out and search; but it gives them no information as to where they should search. Von Frisch found that bees from quite a small hive, in hilly country, when stimulated by the dance to go searching, would find his little sugar-water dishes put out in the meadows more than half a mile away from the hive. It is known that bees from larger hives in flatter country will visit flowers two or three miles off; and doubtless this represents the distance to which they will search. Take the sugar-water away soon after it has been first found, and the bees behave

as they would when a natural source of nectar fades; they dance no more on returning to the hive, and sit at home; and no fresh bees are stimulated to the search.

If instead of a dish of sweet liquid we put out one containing layers of blotting-paper moistened with sugar-water, the bees have great trouble in sucking it up. Apparently the poorness of the supply reacts on their feelings; at any rate, such bees no longer dance when they get home, but simply give what they have got to their younger sisters, and return straight away to the dish. The same happens in nature when a source of supply is drying up and the bees have to visit an unduly large number of flowers to get a load. It would be uneconomical for all the battalions of the hive to be mobilized for a skimpy supply of nectar. And through this simple arrangement—that the bees dance when they have had an easy time getting food, and do not dance when they have had trouble or difficulty—a rough proportion is ensured between the richness of the supply and the number of workers that turn out. So on a cold day, or at a season with few flowers, only occasional scouts will be going out from the hive. But if they find anything, their return sets a number of others in motion.

This, however, is only the A B C of the bees' code. Now come the subtleties. We proceed to attract a few bees to a dish of sugar-water as before; but we stand the dish on a piece of paper on which we have put a few drops of some strong scent, like peppermint-oil. We then put out a number of other dishes, two or three also perfumed with peppermint, others with other strong scents (essential oils are the best, such as oil of thyme or jasmine, bergamot or lavender), still others without any addition of scent. And now we find that only those scented with peppermint will attract any visitors; the rest are neglected. The experiment works equally well with natural flower-perfumes. In place of the artificial dish, we use a bunch of flowers, say phlox, each flower filled with a drop of sugar-water to ensure abundance of supply. Then, when a few bees have found this, we set

out other bunches of phlox not provided with sugar-water, together with bunches of cyclamen. Some bees are busy on every phlox posy, but leave the cyclamens strictly alone, even if they are stood close alongside the phloxes. This is all the more remarkable since phloxes are adapted only to moth visits, and the short-tongued bees cannot reach the nectar in their deep corolla-tubes. Yet once the artificial treatment of one bunch of phloxes with sugar-water has associated phlox-smell and food-supply, the bees go on visiting all the phloxes they can find, searching busily for the nectar which ought to be there by all the rules of the game, but isn't. After this has been going on for a time, we substitute for the sugar-watered bunch of phloxes a similarly treated bunch of cyclamens; gradually the number of bees on the other phloxes diminishes, and the cyclamens begin to be visited, until in an hour or so all are searching cyclamens. You can vary the experiment as you like; any scented flowers will do—beans or thistles, gentians or vetches—the result is always the same. The scent of the flower clings to the bees' hairy abdomen; the trail of workers behind a dancing bee returned from honey-gathering is sniffing at her (if the word sniff be permitted of antennæ) to get her adherent flower-scent.

Now we see that the apparently inconvenient arrangement by which the dance of a successful nectar-gatherer sends out other bees in all directions and not only to the original source of supply, is seen to be admirably adapted to the realities of the situation. The recruits are sent out in all directions; but they are only searching for flowers of one particular kind. In nature many plants of one kind will begin to bloom all over the place at about the same time. Thus the discovery of a single plant freshly in bloom will set large numbers of bees searching the countryside for others of the same sort. The method is as good a one as could be devised for exploiting as rapidly and fully as possible the different sources of honey which succeed each other during the summer season.

Finally, a further subtlety ensures that there shall be no undue waste of energy. We put out two dishes of sugar-water at the same distance, but in different directions from the hive. Each is soon discovered by a few bees, which then remain constant to their own source of supply. In place of one dish we then substitute a poor supply, in the shape of blotting-paper barely moistened with sugar-water. The bees from this dish, as we have seen, will not dance when they return to the hive. But those from the other dish will dance, and their dances stimulate new contingents of workers to fly off and search. We should expect that equal numbers of these fresh workers would visit both sources of food; but this is not so—the visitors to the moist blotting-paper number not more than a tenth of those that come to the easily available food. By close observation, followed by detailed experiments into which we cannot go, the reason for this was found. The different scents of different flowers act as so many signals in this code. But the worker-bees themselves also have a say in the matter. They, too, have a "scent-sign"; they can add this scent to that of the flowers, or they can withhold it. When present it emphasizes what the flowers have to tell; its absence weakens their appeal. The worker-bees have two scent-glands near the tip of their abdomen. These are usually tucked away inside the body, but they can be extruded, and then exhale a scent which to human nostrils smells like the plant called balm. When they are feeding at a rich source of supply, be it dish or flower, they keep on dabbing with these at their surroundings, and before settling they usually fly about for a little, impregnating the air with this scent of balm.

This scent is the emphasis-note in the bee code. When bees are on the search for a flower with a particular scent, they will be moderately attracted by the scent alone, but they will be strongly attracted when the flower-scent is thus underlined and reinforced by bee-scent. This fact ensures that when a group of flowers has been thoroughly exploited by bees, it shall not have the same attraction for newcomers

as flowers already discovered but not yet fully spoiled of their nectar.

This seems to exhaust the bees' code about nectar. But nectar contains no nitrogen, and nitrogen is as necessary for the repair of bee bodies as of our own. Flowers also produce pollen; and pollen is rich in nitrogen. Accordingly pollen-gathering is just as important a part of a bee's activities as honey-sipping. Nectar and pollen between them make up the whole of a bee's dietary. When a bee is going out after pollen, she first takes a little honey in her crop from the stores at home. Arrived at a flower, she scratches the pollen off the stamens with jaws and front legs, meanwhile bringing up a little honey from her crop to make the dusty yellow powder sticky. Her feathery body-hairs also catch pollen, so that she soon gets floury all over. With the elaborate combs on the much-enlarged first foot-joint of her hind-legs (as in other insects her tools are part of her body), she rakes this pollen-flour off; then she rubs her hind-legs together below her body, and by the aid of the wonderful bit of machinery at the joint just above the combs the pollen they have collected is pushed through on to the outside of a joint next above, which is hollowed out into a shallow trough bordered with long springy incurved hairs, and acts as a pollen-basket. With her middle pair of legs she pats the accumulating pollen into shape, until eventually she is carrying two great pollen-masses, each nearly as big as her head. So home to the hive, where she strips off the pollen-masses into a pollen-cell, leaving them to be pounded tight by younger bees; and then back for another load.

The division of labour in the hive goes deep. Bees that go pollen-gathering rarely search for nectar at the same time. And, like the honey-gatherers, they usually restrict themselves to one flower at a time. The methods by which their activities are regulated turn out to be extremely similar to those we have just set forth for the honey-gatherers. When they come back to the nest after a successful trip, they execute a dance (which is as distinct from the honey-dance as a waltz

from a one-step), and this stimulates others to go pollen-hunting. The surprising new fact here discovered by von Frisch is that each kind of pollen has its distinctive scent; this is different from the scent of the flower as a whole, which is usually exhaled by the petals. While the nectar-gatherers are guided by flower-scent, the pollen-gatherers go entirely by the smell of the pollen. This was prettily proved by cutting off the stamens of two different flowers, like campanula and rose, and putting the stamens in the wrong flowers. When a campanula with rose-stamens was provided and a few workers came pollen-gathering at it, their dance stimulated the bees at home to go out looking not for campanulas but for roses. Campanulas were not visited; the smell of rose-pollen prevailed over that of campanula-petals. Curiously enough, although the honey-dance and the pollen-dance are quite different, it is the scent adhering to the dancing bee, not the type of dance she executes, which decides the activity of those she stimulates. This von Frisch proved by catching a bee who was drinking sugar-water and sticking a pair of pollen-bags of rose-pollen on to her legs. She flew home and, being agreeably full of nectar, executed the honey-dance; but the bees that were stimulated to go abroad went hunting pollen in roses. As with nectar, the pollen-gatherer who finds but scanty pollen does not dance on her return; but if pollen is abundant, she underlines the fact by scenting the flower and its neighbourhood with her own scent-organ.

The bees' code thus consists, first of twice as many "signs" as there are kinds of flowers in the neighbourhood adapted to being visited by bees; each flower contributes one sign through its general scent, another through the scent of its pollen. The colours and forms of the flowers also have to be learnt by the bees; they enable another sense to be used in the search. This mere signal-list is converted into a means of providing information by the bees themselves—the dancing after a successful trip, and the imprinting of their own scent on plentiful sources of supply.

Doubtless, as von Frisch says, there are many other things to learn about the signalling of bees. The gathering of pollen and nectar is but one of their many activities; and there must, it seems, be methods of conveying information about comb-building, grub-feeding and other things which are done inside the hive. Here a fruitful field for experiment remains.

Certain central parts of the comb are reserved for the developing brood, with a zone of pollen-cells round them, and the honey-cells filling up the rest of the space—a lucky arrangement, since it enables the bee-keeper to provide us with pure honey-comb without admixture of grubs or pupæ.

When the hive's population has increased to a certain size, the workers begin raising a half-dozen or so grubs to be queens. A few days before they are due to hatch, the workers take a further decision; after a time of unaccustomed restlessness, about half of the thousands, filling their crops with honey from the stores, fly out in a wild cloud of circling, buzzing life, together with the old queen. Soon the queen settles on a branch and all the flight settles round her in a dense cluster, pounds of bees in a solid mass, constituting a swarm. A few scouts are busily flying about looking for suitable spots for a new nest, and if the bee-keeper does not speedily come and coax the swarm into one of his own hives, he will have the chagrin of seeing the cluster resolve itself once more into a cloud and fly away out of sight.

Among the population left behind, a new queen hatches out, and after a week or two flies out on her nuptial flight, is fertilized once and for all by a single one of the pursuing drones (the race for reproduction between the rival males has led to their possessing powerful flight and very large eyes to keep the mounting queen in sight), and returns to the hive, which she will never leave save at swarming-time. If the population is only moderate, the workers kill all the other queen-pupæ. But if it is still large, the first-hatched of the young queens will depart with a new swarm, and then

the workers keep the other queens in their cells, making a little slit in the roof through which the prisoners stick out their tongues to be fed, and keep the first queen away from them; otherwise she would sting them to death before their emergence, for, unlike the queen ant, the queen bee tolerates no rivals.

As autumn draws on, the attitude of the workers towards the drones undergoes a change. As long as new swarms were possible and there might be new virgin queens to fertilize, the drones are carefully tended and fed (they are incapable of getting food for themselves from flowers), even if they chance into a strange hive. But now they begin to be bullied and nipped, and the workers pull them roughly about and throw them out of doors. They try to make their way in again to food and shelter, but are greeted with more bites and even stings. And so gradually, some by starvation and some by cold, some stung to death, this one-sided sex-war ends with the death of all the drones, and the community, now solidly female, settles down for the winter.

In some ways the hive-bee communities are not so highly organized as those of ants; they have only one neuter caste, and their rigid dependence upon flowers for their food has prevented any such marvellous radiation into many ways of life as took place during ant-evolution. But in their buildings they are pre-eminent, and their storage-system is better developed than in any other invertebrate animals. Their remarkable method of giving information so as to exploit to best advantage a great number of kinds of flowers also stands alone, though we can feel sure that fresh observations will reveal something analogous among ants and termites. But, as with ants and termites, there is no real comparison to be made between their communities and those of man. The two organizations are of different kinds, and rest on different foundations. The successes of human communities have been gained by abandoning as far as possible all the things to which the successes of insect communities are due.

The power of automatically performing unlearnt actions, which is the basis of the acts of bees or ants, in man is nearly absent; individual flexibility and indefinitely growing community-experience take the place of rigid behaviour fixed by inheritance.

CHAPTER III

THE EVOLUTION OF BEHAVIOUR IN VERTEBRATES

§ 1

The Vertebrate Nervous System

WE now leave the arthropods and their elaborate instinctive life and proceed to consider the evolution of that type of brain which is characteristic of the vertebrata and which leads up to and culminates in our own.

We shall have to go somewhat more deeply into anatomical detail than we have hitherto done. The human mind can be properly understood only if one has a knowledge of its material substratum, the brain. That brain is a very complicated organ, and though the triplex author will simplify his account as far as he possibly can, sparing his reader every technicality that can be spared, yet, even so, what follows will need close and attentive reading.

To begin at the beginning: all vertebrate animals are made on the same plan; all vertebrate brains consist of the

same chief parts, although, as we shall note, the different classes vary enormously in their elaboration of detail and in the relative emphasis which they lay on the different brain-regions. We will start with the earliest and simplest phases of development.

In a young embryo, the first parts of the nervous system to appear are the great central exchanges, the brain and spinal cord, and, curiously enough, these originate as a tube of skin. We will choose that primitive relative of the vertebrates, the lancelet, as an illustration of this point, for it lays eggs that contain very little yolk, and its development is therefore comparatively straightforward. In higher vertebrates there

FIG. 31.—THE FIRST STAGE IN THE GROWTH OF THE NERVOUS SYSTEM.

are various complications due to the presence of vast yolk stores, or to the growth of embryonic membranes, which we will do our best to ignore.

An early lancelet embryo, five or six hours after fertilization, is a roughly egg-shaped object, just visible as a whitish speck to the naked eye. If we were to cut it across, as cucumbers are cut across, the cut end would look like Fig. 31. The body is made of two layers of tissue, each only one cell thick. The outside layer (stippled) is the skin of the embryo. The inside layer (shaded) is the wall of its digestive tube; the cavity in the middle is the digestive cavity. Now it can be seen that the part of the layer which lies along the creature's back is a little thicker than the rest (shown by a darker stipple in the figure). This part is to become the nervous system. The skin is just beginning to grow up outside it, along its edges.

Fig. 32 is a similar slice of another lancelet embryo, about twenty hours older than the first. Several important changes have taken place in this brief interval. The one that most concerns us is that the rudiment of the nervous system has been overgrown altogether by the skin, and it has rolled up to form a tube which runs along the whole creature, from end to end. But while this special bit of skin has thus been turning into a spinal cord, a rather similar change has befallen the part of the wall of the digestive tube which lies nearest the creature's back. It has separated off from its fellow-cells and now lies as a cylindrical rod, seen in the

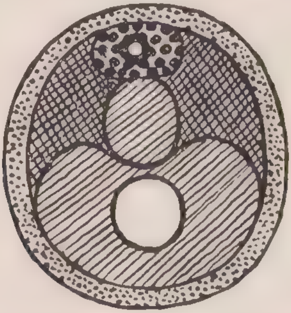


Fig. 32.—The Second Stage in the Growth of the Nervous System.

figures as an oval shaded area, underneath the nerve-cord. This is the notochord—the elastic rod that serves as a backbone for these primitive animals. We also note a third change. A new layer of tissue has appeared between skin and digestive tube (it arises as an outgrowth from the latter), and from this middle layer, shown cross-hatched in the figure, the muscles, blood-vessels, and connective tissue of the lancelet will develop.

In the higher vertebrates also, the fact that the nerve-cord arises as a strip of embryo skin which separates off from the rest and rolls up to form a tube, can be demonstrated, although, as we have already said, there are complications. The hollowness of the central nervous system persists

throughout life. If we cut across the spinal cord of an adult man or woman, the cut surface looks like Fig. 33. On examining it closely, a tiny hole can be seen in the middle. This narrow channel, which runs right along the spinal cord, is the remains of the relatively larger cavity in the embryo spinal cord, and corresponds to the bore of the nerve-tube in the lancelet. In the head it opens into a series of spaces, to which we shall return.

The channels and cavities inside the central nervous system are filled with lymph-like fluid, and they provide one of the ways by which nourishing substances can reach the brain-tissue. But apart from their utility in that direction they are of considerable interest, for they are a unique characteristic of our phylum. No other animals but vertebrates have hollow brains. The brain of an insect is a solid lump of nervous tissue. It is at least possible that this fact accounts for the superior mental development of vertebrates, for, as we shall note, this primitive tube has a way of blowing itself out here and there into pouches, with thin sheets of nervous tissue as its walls. This is a point of importance. Where-ever brain-tissue collects together into dense, solid masses, whether in our own brains or the brains of insects, its working is stereotyped and automatic; apparently an efficient apparatus for plastic, educable behaviour can only develop if the grey matter is spread out thinly. So by making such spreading possible, the primitive hollowness of the vertebrate nervous system enabled its possessors to dominate the world.

There are one or two other significant facts about the spinal cord of an adult vertebrate. First, its substance is of two kinds. Most of it is white, but there is a central core of grey matter (shown stippled in Fig. 33), which has roughly the shape of an H in our cross-cut. As with the brain, the grey matter of the spinal cord is the more vital part; this is where the living telephone exchanges are situated. The white matter simply consists of the telephone wires—of bundles of nerve-fibres running from point to point, mostly up and down along the length of the cord. Moreover, the H-shaped

arrangement of the grey matter is characteristic. The two horns of the H which point towards one's back (upwards in the figure) are receiving stations; it is here that the nerves from sense-organs in the skin, muscles, and so on, deliver their information. The two horns which point towards one's belly (downwards in the figure) are transmitting stations,

Fig. 33.—The Human Spinal Cord cut across, and magnified about eight times.

whence nerves run away to muscles, glands, and so forth, and control their activities. Another point seen in the figure is that two deep clefts, front and back, divide the spinal cord almost completely into halves, one to each side of the body.

This central tube, then, is the first part of the nervous system to appear in an embryo, and from it the nerves presently sprout, growing and branching out through the

body as the roots of a young seedling grow and branch out into the soil.

We have examined the spinal cord in some detail because the brain is really only the front end of the spinal cord made bigger and more intricate; and we can understand it more clearly by studying its derivation from this simpler part. There was once a medical student who described the brain as "a bit of spinal cord with knobs on." The lancelet has

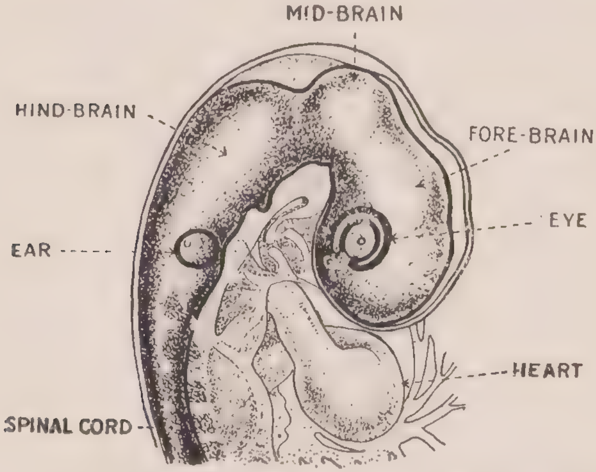


FIG. 34.—THE HEAD OF A CHICK, TWO DAYS AFTER FERTILIZATION.

hardly any brain; the front end of its spinal cord barely differs from the rest. This is because it has few special sense-organs on its head; it lacks eyes, ears, and nose. Moreover, it is jawless and feeds by means of a filter in its throat, which is largely automatic and independent of nervous control. There would be little for the brain to do.

From an ancestor not unlike this we are descended. First special sense-organs developed, and then came the jawed mouth with a definite, discriminating bite instead of a continual automatic sifting of the water. Thus arose the need of

a brain to control the jaws and to receive the reports of the sense-organs. As the latter became better and better developed, the brain became more and more dominant over the rest of the central nervous system. It grew to be the best-informed part of the whole organization; gradually the other parts came to subordinate themselves, to send their own sense-information up to this main centre, and to take instructions from it.

In a vertebrate embryo, the brain first appears as a widening out of the front end of the nerve-tube. Strictly speaking, there are three swellings, not one, and they lie just behind each other. They are called the fore-brain, the mid-brain, and the hind-brain. Fig. 34 shows in profile the head of a chick embryo, about two days old. The front end of the nerve-cord curves forward like a crook, for the chick is hanging its head on its chest. The fore-brain is a hollow swelling, and the right eye can be seen lying over it. The mid-brain is another hollow swelling at the bend of the crook. Behind it is the hind-brain, and that melts gradually into the spinal cord. All these divisions run into each other without sharp boundaries and their cavities communicate freely, for they are only local inflations of the primitive nervous tube.

That is the vertebrate brain in embryo. In later development the three parts take different courses, and each grows in its own characteristic way. To illustrate the state of affairs in the adult vertebrate we choose the brain of the frog, which is drawn from above and from the left side in Fig. 35. It is a fairly primitive brain, and shows all the more important parts very clearly. A mammalian or human brain, although perhaps of more immediate interest to us, would be much less suitable, because in these higher types the two cerebral hemispheres grow enormously and overlap the other parts, so that their relations are hard to make out. We shall consider them later on. Let us take the three main divisions of the frog brain one by one.

The hind-brain is not clearly marked off from the spinal cord; the latter gradually broadens out into the former.

Just as the spinal cord is a subordinate controlling centre with nerves running to the trunk and limbs, so the sides and floor of the hind-brain are subordinate centres with nerves running mainly to the face and throat. The movements of the jaws (and of the gills in a fish) are controlled from here. But there is a curious nerve called the vagus (" The Wanderer ") which differs from the rest ; it runs back into the chest and belly and helps in the regulation of the viscera.

The roof of the hind-brain is, however, very characteristic (by " roof " we mean the part lying uppermost in a quadruped or a fish in the natural posture). In front, just behind the mid-brain, it sprouts out into a special mass of brain-tissue, the cerebellum. This, as we have seen, is an organ concerned with balancing the body and keeping it poised. In that flat, automatically stable creature, the frog, the cerebellum is small, as our figure shows ; but in birds that must fly, or mammals with bodies poised aloft on pillar-like legs, it is large and complicated. It is no accident that such an organ should have developed in this part of the brain, for here the nerves from the ear arrive, and the ear includes the most important sense-organs of balance in the body.

Just behind the cerebellum is another peculiar region, where the central canal comes up to the surface and spreads out as a wide, shallow trough. Over this the roof of the hind-brain is not nervous at all, but an extremely thin film of living tissue. Outside it is a dense network of blood-vessels. The reason for these dispositions is not far to seek. Oxygen and food substances diffuse from the blood through the membrane into the fluid inside the cavities of the central nervous system, and this helps considerably in fuelling and victualling the brain. The thinned-out part of the roof of the hind-brain is lightly stippled in Fig. 35.

The mid-brain has thickened, nervous walls, so that its central canal is in most animals narrowed like the canal in the spinal cord. The most important centres lie in its roof, and bulge up as the solid " optic lobes," of which there is usually one on each side of the brain. In most vertebrates these optic

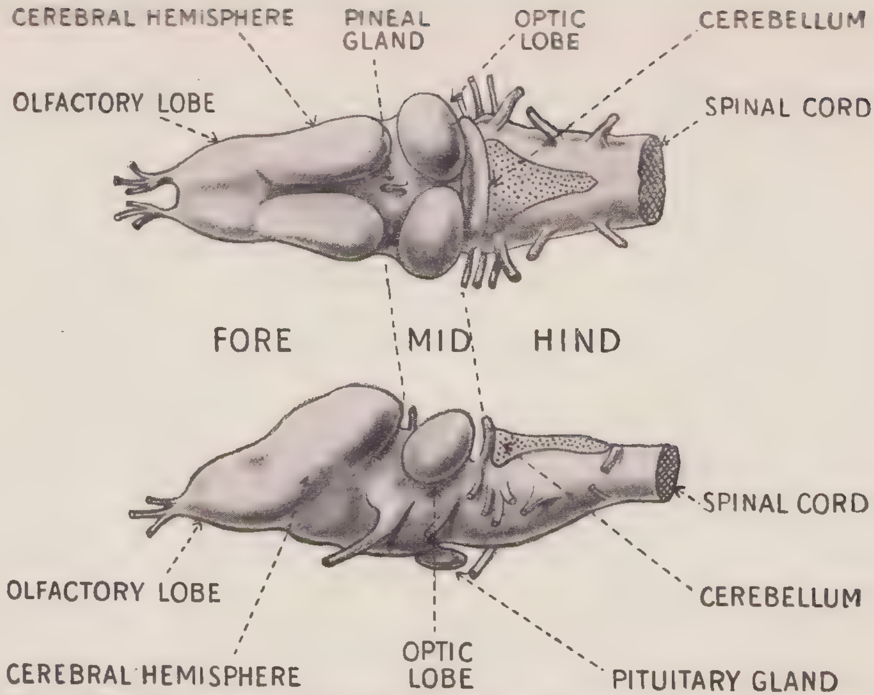


FIG. 35.—THE BRAIN OF THE FROG, SEEN FROM ABOVE AND FROM THE LEFT SIDE, TO ILLUSTRATE THE CHIEF PARTS OF THE VERTEBRATE BRAIN.

The cross-hatched area shows where the brain has been cut away from the spinal cord. The numerous little stumps are nerves, cut across a short distance from the brain.

lobes are the chief centres to which the nerve-fibres from the eyes take their course, and they serve for that important function, visual reception. They are very conspicuous prominences in the frog. But in mammals they are superseded by the hollow cerebral hemispheres, and suffer a corresponding diminution in size. Moreover, the mid-brain is the seat of origin of nerves to the muscles which move the eyeballs, and is the main controlling centre of their movements. These are its best understood duties, but there are others which still await full analysis. In particular, the hind-brain, like the spinal cord, seems to be concerned in essentially unconscious and mechanical activity, but with the mid-brain we come to a higher plane. Much of the activity of this region also is simple automatism, at least in ourselves; but in fishes and frogs the mid-brain seems to do many things that we relegate to our cerebral hemispheres, and even in mammals it may perhaps be the seat of conscious sensations of pleasure or pain.

So far the parts of the brain are fairly straightforward, and similar, except for very minor variations of detail, in all backboned animals from fishes to ourselves. But the story of the fore-brain is more difficult. Here the organs of intelligent thought arise; here are found the greatest divergences between the members of the vertebrate series. And the forebrain has a somewhat confusing way of sprouting out at various points into hollow outgrowths, which are not always nervous in function.

Very early in the development of an embryo it can be seen that the fore-brain is swelling out into two additional hollow bulbs, one on each side, much as the sides of the reader's face will swell out if he shuts his lips firmly and slowly puffs out his cheeks. These bulbs sprout out more and more distinctly and their connection with the middle part of the fore-brain narrows down to a stalk like the neck of a flask. These two bulbs are not going to be parts of the brain at all; they are the first rudiments of the eyes. They grow nearer and nearer to the skin, and as they approach it the skin changes curiously and gives rise to the lens and cornea. The outgrowths from

the brain become the retina and the black pigment-layer outside the retina; their stalks grow solid and become the nerves which carry sight-impulses from eye to brain.

Meanwhile, two smaller bulbs with thicker walls grow out from the extreme front end of the fore-brain. These ultimately will be connected to the nose by nerves, and they are the brain centres at which the impulses of the sense of smell first arrive. They are called the olfactory bulbs, and are seen at the front end of the brain in Fig. 35.

Another and even stranger growth springs from the floor of the fore-brain. A hollow protrusion, rather like the finger of a glove, sprouts out and grows downward and backwards towards the roof of the mouth. As it does so a bit of the embryo's palate separates itself off from the rest and moves up to meet it. The two organs, the bit of brain and the bit of mouth, unite together to form a compound organ, the pituitary gland. That the brain should participate in this adventure is altogether strange, for the pituitary gland has nothing to do with nervous activity, neither is it a sense-organ; as we described in the first Volume of this Series, it is one of the ductless glands or organs of internal secretion. It influences growth and the general chemistry of the body; in frogs it plays an important part in the animals' changes of colour.

An interesting parallel case of entanglement between the nervous system and the ductless glands is found in another region of the body. The nerves running out from the central nervous system divide into branches of two kinds. Some run to the muscles of the limbs, trunk, face, and so forth which are under immediate voluntary control, and also to sense-organs in the skin and in deeper parts concerned with the position and movements of the body. These nerves execute our ordinary conscious movements. But others go to our more unconscious regions, and supervise such activities as the writhings of the digestive organs, the speed and force of the heart-beat, the tension of the muscles in the arteries, and so forth. Moreover, the nerves of this second group swell out

here and there into knot-like swellings—subsidiary exchanges, on the telephone analogy—where a certain amount of routine work can be done without bothering the central nervous system.

Now, in a developing embryo, the rudiments of the nerves of this second group can be traced ; and it can be shown that as they grow the knot-like swellings on them bud out tissue of a different kind. Besides giving rise to nerve-tissue, these germs give rise to a set of little ductless glands. In later development, most of the glands thus formed are gathered together into two main masses, one lying on each side of the backbone just in front of the kidney, called the adrenal glands. (As a matter of fact, the adrenal gland is a double structure with a main central mass surrounded by a distinct peel ; the centre arises as we have described, while the peel has a different origin and different functions. Why they thus come together nobody knows ; and the fact is a complication which does not concern us now.) This case is, however, not so puzzling as the case of the pituitary gland, for the adrenal glands help in regulating the organs of digestion, circulation, and so forth. They are a labour-saving accessory of the nervous system. In a crisis when the organism has to fight or fly for its life it is obviously advantageous to suspend the operations of the digestive organs so that all the bodily energies can be concentrated on the effort ; at the same time the circulation must be speeded up and made more efficient. This is done generally, by sending a single nervous message to the adrenal glands. The glands pour their secretion into the blood and it circulates everywhere, mobilizing the resources of the body as it goes. In the absence of such a device we should have to send special nervous instructions separately to every organ concerned, so these glands effect a great economy of nervous effort.

But we must return to the fore-brain, and take note of the fate of its roof. A large part of this roof is thin and richly supplied with blood-vessels ; like the thin part of the roof of the hind-brain, it assists in supplying the central nervous

exchanges with nutriment. But out of it there grows a little stalked knob, the pineal gland, showing very clearly in Fig. 35. This, like the pituitary gland below, is an organ of internal secretion. But it has a curious history. At one time the vertebrate stock had at least one eye—probably two—staring upwards from the middle of the head; to this day traces of those eyes can be made out in many amphibians and reptiles and in the lamprey, that relic from a remote past when our stock was jawless. Apparently the pineal gland is a fore-head eye which first became blind and useless and then (at least in the higher vertebrates) was turned to another purpose, and made into a ductless gland.

Thus the brain, like the rest of the nervous system, starts off in the embryo as a specialized bit of skin. But besides nervous tissue, this rudiment gives rise to two sense-organs, the eyes, and to a whole series of ductless glands. We will conclude our preliminary survey of the vertebrate nervous system by noting some vitally important, dominating ex-changes that appear in the walls of the fore-brain as it grows.

In most vertebrates the fore-brain has only one direct nervous connection with a sense-organ, and that is the nose. We have already seen how the primitive smell-centres push out in front as the olfactory lobes. True, the eye and its nerve grow from the sides of the fore-brain; but the nerve gets connected with the optic lobes in the mid-brain, and to them it sends all its information. Moreover, there are no out-going nerves from the fore-brain to muscles or glands. All the effectors receive their nerves from farther back along the nervous tube. A glance at Fig. 35 will show that the hinder half of the brain (like the spinal cord) is thickly beset with nerves, while the front half is comparatively nerveless. In a word (except for its nerves to the nose), the fore-brain is free from the immediate routine business of receiving information and dispatching replies.

And now, in the light of the things we have already learnt about the brain, let us return to the story of how it evolved. We start from brainless creatures like the lancelet; as the

vertebrate stock evolves, a biting, tasting mouth and a set of highly specialized sense-organs appear, and the front end of the nervous tube enlarges and reorganizes itself to meet the responsibilities thus put upon it.

The mouth and throat come under the supervision of the hind-brain. Here the nerves to their muscles arise; here the reports from the taste-organs are considered. The ears also, and the lateral-line organs that we shall consider in the next section, send their information to this region. The mid-brain enlarges itself primarily in order to receive and analyse information from the eyes; it also regulates the eye-movements. At the front end of the fore-brain a centre grows up where impulses from the organs of smell arrive and are dealt with. Each of these departments of the brain is dominated by a particular sense-organ. Naturally they do not work in isolation and mutual independence; they intercommunicate; they are connected together by nerve-cables running within the substance of the brain, so that their various activities can be brought together and harmonized.

In the lower vertebrates, one or other of the executive departments may stand out over its fellows and become the leading part of the brain. Thus the trout is predominantly a visual fish. Its optic lobes are very large and they receive nerve-fibres from the other sense-centres; all such reports are considered, but the final decisions are made in the optic centres, and impulses from the eye naturally play a dominating part in the conference. The dog-fish, on the other hand, relies more on smell; the olfactory centres at the front end of its brain are enormous, and hither the other regions send their reports. As any keen angler will tell you, a trout has a critical eye for the appearance of the lure. But fly-fishing for dogfish would be a very different game; instead of tinsel and jay's feathers the lure would have to be ornamented by judiciously chosen scents. To take a third example, the carp (which has the gait and general expression of an incorrigible epicure) is a gustatory fish; it has very well-developed taste-buds in its mouth, and here the leading part in determining

its behaviour is played by the distended taste-centre in the hind-brain.

But none of the highest vertebrates allows one sense thus to dominate over the rest. They cultivate them all, and keep a balance between them. Moreover, to guard against any unfair weighting of the scales they hold the conferences in neutral territory. They have developed special parts of the brain which are not under the sway of any one sense-organ, and to these new centres all the others send their reports. The obvious place for these new developments was the comparatively unoccupied territory of the fore-brain.

These new centres may be called centres of correlation, for they are not immediately concerned with reception from sense-organs, or with the dispatch of instructions to effectors. The sensory information is digested by other centres before it comes on to them, and their decisions are carried out by subordinate centres. To draw an analogy with a business organization, the new fore-brain centres are managers and dictate the policy of the body ; the routine business of opening envelopes and writing letters, and even of making automatic reflex replies in easy cases which do not demand special consideration, is done by secretarial staffs elsewhere.

Crude rudiments of these centres of correlation are found in fishes, but they do not attain to their full dominance until we reach the higher land-vertebrates—the reptiles, birds and mammals. They fall into three groups. First, there is a set developed in the side walls of the fore-brain near its hinder end. Chief among these is the thalamus. This structure cannot be seen in Fig. 35, for it does not protrude conspicuously from the surface of the brain ; but it lies at the side between the optic lobe and the hinder end of the cerebral hemisphere. The second set appears on the floor of the fore-brain in front of the thalamus ; it is known collectively as the corpus striatum. As we shall see, this set is the dominating part of the nervous system in birds. The third set is a series of sheets of grey matter which appear in the roof of the front part of the fore-brain. These constitute the cerebral cortex,

which attains its highest development in ourselves. A frog or a fish has no cerebral cortex, and we find its first beginnings in reptiles. The part of the brain labelled "cerebral hemisphere" in Fig. 35 consists largely of the centres which receive smell-impressions and of the somewhat rudimentary corpus striatum. But of all these parts we shall learn more in the following pages.

§ 2

The Mind of a Fish

The first vertebrates lived in water; we ourselves show in our own embryonic development that our bodies are the bodies of fishes turned and twisted about to fit them for a life on land. This is true of our brains, and correspondingly of our minds. Some of our sense-organs are still much the same as they were in our finned ancestors. The smell-cells in the nose, for example, are definitely fishy and will only work if they are immersed in water; so we find in an out-of-the-way corner of the cavity of the nose a special set of little glands, evolved when the vertebrates came on to dry land, whose business it is to secrete a film of moisture over the smell-cells—a tiny vestigial sea for them to work in. So let us throw our imagination back through the eras, and try to get an idea of what it was like to be a fish.

The most arresting difference between the behaviour of a fish and that of a land-vertebrate is the manner of muscular response. Instead of long jointed limbs the fish has a sinuous trunk and a powerful tail; instead of our standing, running, walking, gesticulation, manipulation, and so forth, it has a series of undulatory movements. It does not know the feeling of planting its feet on firm ground, for its weight does not greatly exceed that of the surrounding water; instead it swims through a medium somewhat heavier and more resistant than air, and its muscular energies largely consist in a rhythmical sideways pressing of body and tail against that enveloping substance.

Running along the sides of a fish's body is an important sense-organ that we lack completely—the lateral line. In a dog-fish, for instance, this is noticed as a white stripe along nearly its whole length, from the tail to the back of the head. When it gets to the head it divides into two or three branches, which run about on the cheeks, chin, and snout, and make patterns which vary in different kinds of fish.

On examining the lateral line closely we should see a row of fine pores all along it, but larger and more conspicuous on the head than elsewhere. These pores open into a common canal, which lies just under the skin. Inside the canal there are bunches of sensitive cells rather like the sensitive cells of the inner-ear. As a matter of fact, there are grounds for believing that the ear is really only a bit of the lateral line enlarged and glorified for its special functions—much as our cerebral hemispheres are enlarged and glorified bits of spinal cord. But that is by the way.

Just what this lateral line does is by no means clear. Some writers believe that it detects currents, others that it is sensitive to pressure, others again that it responds to slow pulsing vibrations of the surrounding medium. The most probable suggestion is that it feels the force with which the fish's flanks press against the water. The animal progresses by means of a series of wave-like sideways pushings of great strength and delicacy—for they have to be nicely controlled if it is to go straight. We may assume that it has a delicate sense of the contact between itself and the water, responsive to every slight variation in intensity, and that this sense is one of the regular pervading elements in the background of its mental life.

The eyes of fishes are less well developed than our own, and this is only to be expected, for water is not so favourable a medium for vision as air. Generally it is more or less turbid, either because of suspended mud or sand, or because of the very intensity of minute floating life in it; even in the exceptionally transparent water of coral islands it is not possible to see very far. To a fish distant objects are per-

ceptible as looming shadows—even with our own refinements of the eye they would be little more—and clear vision is only possible at close quarters. Accordingly we find an interesting difference between a fish's eye and our own. We ourselves, when we relax our eyes, focus them on distant objects; that is the natural position of the parts to which they automatically tend, and to examine close objects, as in reading or writing, can only be done by exerting certain little muscles which alter the shape of the lens. But the machinery of accommodation in the eye of a fish is different. Here, in the relaxed position the eye is focused for near objects, up to a foot or so away, and the focusing-muscles work in the opposite direction. By straining their eyes big fishes can focus them on objects up to some thirty or forty feet away. But the precise distance depends, of course, on the size of the fish. Little trout, about six inches long, can see clearly for a foot or eighteen inches. Outside that radius their world is hazy and fades away.

Can fish smell? The point is often disputed, for our noses detect perfumes borne in the air, and on the surface of things, at least, it is hard to imagine a fish as smelling in an analogous way. But the difficulty disappears when we remember the little bit of sea in our noses in which our smell-cells are immersed. Odorous substances from the air have to dissolve in that film of fluid before they can be perceived at all. As a matter of fact, it can be proved that in fishes the senses of smell and taste are as distinct as they are in ourselves. Such substances as we know as odorous stimulate the fish's nose and the information is conveyed thence to the olfactory lobes at the front end of the brain. Substances which are bitter, sour, and so forth and stimulate our own taste-organs are perceived by similar organs in fishes, and in this case the information is received by a centre in the hind-brain. But in a fish there is no reason why the taste-buds should be confined to the mouth, for the whole skin is moist and suitable for their operation; and we do indeed find that many fishes taste with other parts of their anatomy. In cat-fishes, and in the carp

and its relatives, taste-organs are found over the whole body, being especially plentiful in the little " feelers " and barbels that often project downwards from the chin and are used to examine the mud and to detect any smaller animals or other appetizing morsels. If you quietly drop a bit of meat close to the flanks of a cat-fish, the animal will twist round and snap it up at once, in virtue of its diffuse powers of taste. Some fish even taste by means of filaments trailing in the mud from their hind-fins.

Moreover, there is a third chemical sense in fishes, distinct from these two. This so-called " common chemical sense " is stimulated by various irritating substances and by alterations in salinity, and it is apparently much less discriminating than taste or smell. It has no specially constructed sense-organs, but depends, as pain depends, on free nerve-endings in the skin. But it is a sense distinct from pain. Newts show the same common chemical sense. In the higher land-vertebrates it is largely lost; the dry, thick skin that they find necessary to prevent excessive evaporation of water makes such a sense an impossibility. But just as smell and taste linger on in special moist corners of the body, so the common chemical sense lingers in such places as the inside of the nostrils and the cornea of the eye. The smarting of the eyes, nostrils, and mouth, produced by ammonia vapour, is an instance of its operation.

For the chemical senses, then, fishes are well equipped. Their ears on the other hand, are primitive. They have, of course, the apparatus of three semi-circular canals at right angles to each other with which all vertebrates balance themselves, but the part which corresponds to our cochlea is so poorly developed that it is doubtful whether they can hear sounds at all. The fish ear lacks the apparatus of outer-ear, ossicles, and ear-drum that collects vibrations and transmits them to the inner labyrinth in ourselves; embedded in the skull, the latter can only be stimulated by vibrations that have passed through the tissues of the head. Fishes can be trained to come for their food when a shrill whistle is blown or when

a bell is rung; but Parker has shown that similar reactions can be brought about by jarring the side of the aquarium with a pendulum as stimulus. In both cases the response is abolished by cutting the nerve to the ear. It may be that a sound affects the fish like a sort of fluid jolt, a sudden disturbance of the water, and no more than that. Their ears are, perhaps, more tactile than auditory.

In the matter of other senses—touch, pressure, pain, and so on—fishes are probably endowed very much as we are. However, although they are sensitive to temperature, they can seldom experience such sensations as the sudden warmth of a ray of sunshine or the chill of a breeze, because of the very uniform temperature of the water in which they live.

As for the intelligence of fishes, most people who have studied them carefully are agreed that they are stupid and learn but slowly. One or two instances of their educability are worth quoting. Triplett kept a pike in an aquarium with a number of smaller fish, but he separated the two by means of a glass plate. Soon the pike learnt that to leap at the other fish was to get a sharp blow on the nose—although it could not possibly understand the reason, for the glass plate was perfectly invisible. Presently the glass plate was removed, and the pike swam round with the other fishes. But it never made any attempt to seize them.

Thorndike put fish at one end of a glass tank, with an attractive shady corner with food in it at the other. In between were a series of glass partitions, each with a hole in it in a different place. The fish felt their way to the other end of the tank by bumping up against the glass plates and, after a considerable amount of trouble, finding the openings and getting through. But after a number of trials they learnt where the invisible openings were situated, and swam directly to the goal. Recently Bull has begun to analyse the learning-powers of fishes by means of Pavlov's method of conditioned reflexes (of which we shall learn more hereafter), and he is getting surprisingly good results.

A fish, then, can learn a certain amount, albeit with labour

and slowly. But it lives in a curiously circumscribed world. Light soon loses itself as it travels through the water; sound-waves also travel badly in the heavy medium. Even smell is a short-distance sense in a fish and not a long-distance sense as it is in a dog or a deer. Water currents are very different from breezes, and fish sniff at things and thus find their prey, but do not scent it from afar. One of the most important things that happened to the vertebrate mind when our stock came on land was an enormous extension of the radius of the perceptible world.

§ 3

The Amphibian Mind

Before we go any further we must take up again our account of the vertebrate nervous system, and note an important difference between the fore-brain of all land-vertebrates and that of most fish. The rest of the brain need not detain us, for it is very much the same in all vertebrates; they all have underlying their conduct the same basis of automatic reflex behaviour. As we proceed the fore-brain will force itself more and more exclusively on our attention.

Fig. 36 is a rough diagram to show the essential points at issue. On the left is the fore-brain as it appears in most fish. It is drawn from above. The front end of the mid-brain (M) is seen behind; this leads into a hollow swelling (F) which is the fore-brain. At its extreme front two pouches (O) have grown out; these, as we have seen, are the olfactory lobes. The chief nervous exchanges are indicated as stippled areas in the figure. First there is a mass of tissue concerned with the reception and analysis of impressions from the nose. This appears as a U-shaped area coming back from the olfactory lobes. In most fish it lies as a conspicuous swelling on the floor of the fore-brain, and near the middle line. At the sides of the fore-brain some other centres can be seen, especially near its hinder end. These are not intimately bound up with any of the sense-organs; they are the rudiments of those

superior centres whose evolution we discussed at the end of § 1 of this chapter.

Contrast with this the drawing on the right, which is a general scheme of the fore-brain in land-vertebrates. Instead of being a single chamber the fore-brain has nearly divided itself into two, so that now it has the shape of a Y. Behind is a region (T) called the between-brain, which remains undivided through life. In front of this is the divided part; its two halves are called the cerebral hemispheres. (They are clearly seen in Fig. 35, but the frog differs from most land-vertebrates in having its olfactory lobes joined together in the middle line.) Properly speaking, a fish has no cerebral hemispheres, although it has the undivided parts corresponding to them.

Just why the front part of the brain should bisect itself in this way is not known; but the resulting Y-shape of the fore-brain runs through all the animals with which we now have to deal. Oddly enough, it first appears in lung-fishes, those strange links between water-life and land-life.

Notice how the main nervous exchanges come to lie when the partial bisection has been done. Those concerned with the sense of smell have been divided by the incision and now lie in the inner wall of each hemisphere, and rather towards its floor. In that position what we may call the "nose-brain" is found in all vertebrates from the amphibians up. The superior exchanges are enlarged and elaborated in the brains of land-forms, and in our diagram we can distinguish two pairs of these. The first pair lie one in each of the cerebral hemispheres; they are thickenings of the outer halves of the floors of the hemispheres. Each of these is called a corpus striatum. The second pair lie at the sides of the hinder, undivided part of the fore-brain; each is a set of three or four centres, of which the most important is the thalamus.

This brings us to the fore-brain as it occurs in the most primitive land-animals, the amphibians. The cerebral hemispheres are largely occupied with the sense of smell. Over most of the walls of the fore-brain, where they are nervous in

structure, the grey matter lies up against the internal cavities, and outside it is a layer of white matter. That is to say, most of it is organized on the same plan as the spinal cord.

Only in the smell-brain, on the inside walls of the cerebral hemispheres, is there a tendency for the grey matter to move away from the primitive position and to spread evenly through the whole wall of the brain. This is a foreshadowing of a most important development that occurs in higher

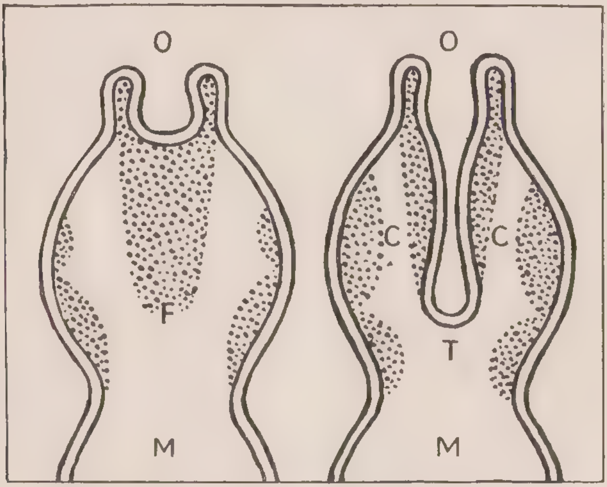


FIG. 36.—THE EVOLUTION OF THE FORE-BRAIN (SEE TEXT).
(M) is the mid-brain, (F) the fore-brain, (O) the olfactory lobes, (T) the between-brain, and (C) the cerebral hemispheres.

vertebrates—the growth of layers of grey matter on the surface of the brain.

Corresponding with this primitive arrangement of the highest centres of the brain we find that the amphibians are stupid creatures, with a certain endowment of instinct but with very little intelligence or educability. Those who have made pets of newts or frogs testify to the general witlessness of the creatures. There is, however, a distinction between

the tailed and tailless amphibians. Newts and their relatives still wriggle precariously on the border-line between water and land; their tails are not very powerful for swimming compared with the tails of fishes, and their limbs are small and feeble. Frogs and toads are altogether more competent creatures. Except for their larval history, they are true land animals with powerful legs. They are not nearly so dull as newts; and their brains (especially their optic lobes and thalami) show a better development of the leading nervous exchanges. But even frogs are morons compared with reptiles.

Nevertheless, a study of amphibian behaviour illuminates the contrast that we have drawn between life in water and life on land. The lateral-line organs, for example, linger on in aquatic amphibians—in tadpoles and many newts—but disappear in the definitely terrestrial frogs. Again, true hearing and the voice appear as the vertebrates move into a light gaseous medium which can convey sound-waves adequately. Most newts are deaf and dumb; but frogs have ear-drums, and a single ossicle connecting each drum with the labyrinth of the inner-ear; and frogs, as anybody knows who has lived near a frog-populated pond, have vocal cords of which they make good use. Some such chorus of croaks, trills, grunts, and metallic clicks must have echoed in the warm coal-measure marshes when, with the amphibian, the vertebrate voice first came into the world.

Eyes are small or absent altogether in newts, but in frogs and toads they are well developed, and are the chief sense-organs by which the creatures hunt their prey. Even so, the amphibian eye at its best seems to give a very blurred image. Frogs and toads will not touch their prey unless it moves. A hungry frog sees a fly crawling along; he sits up alertly and takes a few steps towards it. If the fly stops still, nothing further happens; but as soon as it moves again, out flicks the frog's sticky tongue, and the fly disappears. Not only is a motionless insect invisible to the frog, or at least not recognized as possible food, but any small moving object will elicit

the reflex snapping movement. Frogs in a glass jar can be made to snap at the end of a pencil pulled along the glass from outside, and will do so again and again, learning nothing by the fruitlessness of their efforts.

Indeed, although amphibians can be induced to learn under experimental conditions, their powers in this direction are comparatively poor, and cannot play a very important part in their normal life. They live almost entirely by instinct, such as the impulse to snap at any small moving object, which keeps them fed.

Sometimes they have surprisingly elaborate instincts. There is a Brazilian tree-frog called the " ferreiro," or smith (because its voice sounds like slow hammering with a mallet on a copper plate), which builds special little nurseries in the shallow muddy water at the margin of ponds to keep its tadpoles safe. The female, who does the work, plunges down and brings up an armful of mud, and out of a series of armfuls constructs a little circular wall. Observers have described the careful way in which she smooths the inside of the nest with her hands. Another Brazilian tree-frog lives in willows near the water and never comes down even to breed. It lays its eggs in jelly-like masses wrapped up in a sort of nest made by sticking two or three leaves together. As the tadpoles develop the jelly softens and liquefies until finally they plop down into the water below.

The courtship of newts is an interesting display of instinct which any country-dweller may witness by improvising an aquarium. In spring the male develops a magnificent crest on his back and tail and his colouring becomes more brilliant, with patches of black, orange, iridescent blue and white that vary from species to species. Putting himself across the path of a female, he " dances " and waves his crest in front of her, with a curious sideways bend of his body so that his fringes hang almost over her head. Then he turns his back on her, takes a few steps away, and, with violent wavings of his plume-like tail, he very conspicuously extrudes a little white packet containing sperms. If she has been affected by his

courtship she steps towards it as it floats in the water, seizes it in her hands, passes it to her feet and inserts it into the opening of her oviducts.

But these fine elaborations of instinct are behaviour climaxes, occurring only at special times of the amphibian life. Usually, their daily round of feeding and so forth is comparatively simple. They survive individually not so much because of their activities as because of their general timidity and furtiveness. Usually they live obscurely hidden in damp corners; most land-living frogs and toads come abroad at night, and day-frogs often have striking powers of protective colour-change. As a result of their marginal existence on the fringes of water and land, it is interesting to note that less than three thousand species of amphibians are known, as opposed to over five thousand reptiles, thirteen thousand mammals, twenty thousand fishes and twenty-eight thousand birds. The amphibian is on the whole an ineffective creature, neither truly aquatic nor truly terrestrial. Partly in virtue of its slimy venomous skin, and partly in virtue of its prolific spawning, its race manages to muddle along.

§ 4

The Brain in Reptile, Bird, and Mammal

The first land-brains must have been very like the brains of our modern newts and salamanders, the most primitive of living amphibians. In lung-fishes we find very similar brains. It is a simple, inefficient type, as we have seen, and corresponds to a general dullness and limitation of the possible modes of behaviour. In many respects amphibians and lung-fishes are less well equipped mentally than the majority of modern fish. From an evolutionary point of view, they represent a stage when the attention of the stock, to speak very metaphorically, was focused on those alterations which made land-life possible—on the shift from gill-breathing to lung-breathing, with its consequent revision of the whole

layout of the throat, the heart, and the main arteries. It may be their very mental inadequacy which, by putting them at a disadvantage compared with their competitors in the waters, forced them to make these adjustments and come on land.

But when the vertebrate body had been properly fitted for a terrestrial life, when the dry impermeable skin and the protected egg, which characterize all vertebrates above the amphibian level, had been evolved, there arose a new era of intense competition on land. Terra firma ceased to be a refuge for the witless, and, except for a few out-of-the-way corners, became a hard school in which only the nimble and vigorous, or the exceptionally well protected, could hope to survive.

The whole apparatus of behaviour was improved. The vertebrate body was raised from the ground; instead of crawling on their bellies, reptiles began to run, leap, and fly. Sense-organs, and especially the eye and the ear, got progressively better and better. There was a general speeding up of the metabolic processes of the body; the heart and arteries were made more efficient; the lungs became more elaborately honeycombed to increase the rate at which oxygen could be absorbed; the kidneys were reorganized and their ducts were disentangled more completely from the reproductive apparatus than had previously been the case. This general revision culminated in the birds and mammals. Meanwhile there was a necessary correlated increase in the elaboration and efficiency of the central nervous system.

The most essential difference between the brains of amphibians and reptiles is the appearance in the latter of a new way of arranging grey matter in the walls of the cerebral hemispheres. It is a departure of the profoundest significance. In an amphibian fore-brain the grey matter is mostly massed next to the inner cavities in the same primitive position as it occupies in the spinal cord. But in reptiles, and in all higher vertebrates, thin grey sheets appear in the roofs of the hemispheres, separated from their cavities by layers of white matter of varying thickness. In ourselves

the sheets lie right at the surface of the cerebral hemispheres, and they are therefore spoken of as the cerebral cortex (" cortex " means " peel ").

It is important for us to realize the distinctive features of this cerebral cortex. The first is its general design—it is laid out, as we have already stressed, in thin sheets and not in dense masses, and this is necessitated by its highly characteristic microscopic structure. To penetrate into the minute details of that would be laborious and take us further than we need to go. The second point is its position. We saw that the primitive vertebrate brain consists of a series of centres intimately connected either with sense-organs or with groups of muscles, and of tracts of fibres running telephone-like from centre to centre, and enabling them to communicate with one another. But soon special centres of a superior kind are evolved, not dominated by any immediate connection with a sense-organ or an effector, but communicating only with other nerve-centres, not occupied with immediate reception or control, but supervising and regulating the rest of the brain.

Now evidently it is of advantage for such presiding regions to be somewhat aloof anatomically from the subsidiary centres they control—just as it is a good thing to have parliament in a separate building of its own and not mixed up with one of the executive departments such as the War Office or the Ministry of Labour. Herein lies the importance of the roof of the fore-brain as a site of the cortex.

Let us recapitulate very briefly the general layout of the brain to make the point clear. At the front end of the fore-brain lie the nerve-centres connected with the nose. To return to the parliamentary analogy (for the central nervous system is indeed the government of the body state) this is the Ministry of Smells. Farther back, in the mid-brain and hind-brain, are the Ministry of Vision, the Sound Office, the Ministry of Position and Equilibrium, the Ministry of Respiration, the Ministry of Abdominal Contentment, and so forth. These are all routine executive organizations. They communicate with each other by massive tracts of

nerve-telephones; and in particular we may note tracts that run up along the floor and sides of the fore-brain to keep the other departments in touch with the Ministry of Smells.

In the simplest brains, the roof of the fore-brain is not primarily nervous; as we saw in the first section of this chapter, it is mostly thin and nutritive in function. The first superior regulating centres develop along the tracts between the nose-brain and the rest. Here they find space enough, unoccupied by the executive centres; here, also, they are able to inform themselves and to regulate, because of the tracts of nerve-fibres. This is how the thalamus and the corpus striatum arise. But when they have appeared, on the sides and floor of the fore-brain, a new possibility follows. Hitherto the development of the roof into a controlling centre has been impracticable; but now fibres can grow up into it from the corpus striatum and thalamus, and the cortex can develop out of the way of the main lines of communication between ministry and ministry, using the corpus striatum and thalamus as intermediaries for its information and decisions. Once this step has been taken, to develop the human brain becomes only a matter of elaboration and refinement; all the essential zones are present.

The cerebral cortex is found in reptiles, birds, and mammals. Its appearance is a tremendous stride away from simple automatism towards intelligent behaviour. But, curiously enough, its possibilities are only fully exploited in the mammals. For the brain in land-living vertebrates evolved along two different contrasting lines. One leads through the dinosaur-like reptiles to the birds; the other leads to the mammals. For a time they evolved together, but soon they separated.

In the bird development, the principal evolutionary change was the enlargement and complication of the corpus striatum. That part of the brain may be said to culminate in birds. Nowhere else is it so elaborately organized; nowhere else does it outweigh the other parts so markedly in size. But while the floor of the fore-brain was thus undergoing im-

provement, the roof remained thin and the cortex small. In the mammal direction, precisely the opposite occurred. The corpus striatum did, indeed, undergo a certain amount of revision and reconstruction, but the main progressive change was the enlargement and elaboration of the cerebral cortex. As we shall see in a moment, this difference underlies a very striking contrast between the behaviour of birds and that of mammals.

Modern reptiles are more bird-like than mammal-like in their brains. They are, of course, a mixed bunch, scattered and often only remotely related survivors of an enormous group which once dominated the world. But our own stock broke away very early indeed from the main trend of reptilian evolution, and took a different direction. Both from the brains of existing reptiles and from the skulls of fossil ones we can see that all through the Mesozoic Era the dominant vertebrates were enlarging the floors of their fore-brains and neglecting the cortex. This occurred most markedly in the dinosaur stock which led up to the birds, and to which the crocodiles are closely related. The tortoises and turtles diverged at an early date, and in their brains we find the same tendency, but in an altogether less exaggerated form.

Let us illustrate these points concretely, by considering three actual brains. Fig. 37 shows the brain of a lizard seen from the left side; on comparing it with the frog's brain in Fig. 35 the increase in importance of the cerebral hemispheres will be obvious. Already in the frog there is a perceptible tendency for the hemispheres to bulge backwards over the other parts; but in the lizard they have reached to the optic lobes and overlap the between-brain so completely as to hide it from view. Also they protrude upwards more prominently than in the frog. Fig. 38 shows the brain of a bird, from the same side. Here the growth of the hemispheres, both upwards and backwards, is exaggerated, and the optic lobes are pushed out of their way down on to the sides of the brain-stem. Also a considerable expansion of the cerebellum is noticeable; this is because the postural adjustments

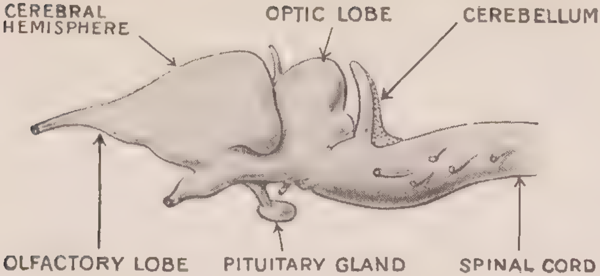


FIG. 37.—THE BRAIN OF A LIZARD.

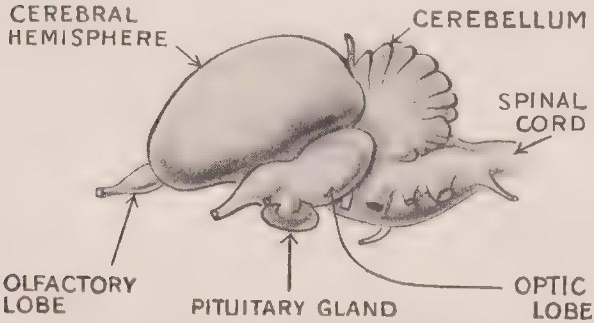


FIG. 38.—THE BRAIN OF A PIGEON.

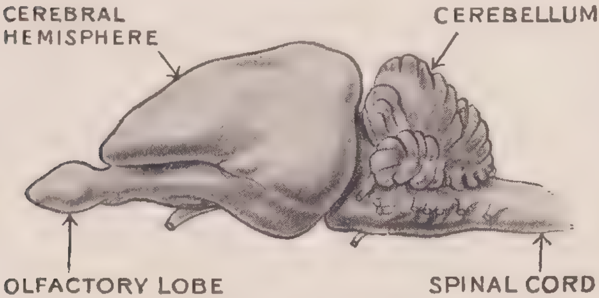


FIG. 39.—THE BRAIN OF A RABBIT.

The brains are drawn from the left side. Compare Fig. 35.

of a bird, flying and walking on two legs, require more supervision than do those of a lizard. The expansion of the cerebral hemisphere in both these brains is due to a great upward swelling of its floor; its roof is comparatively thin and has been bulged out by this great swelling below, much as Everyman's bedclothes bulge upwards when he lies on his back and raises his knees. Finally, Fig. 39 shows the brain of a rabbit, a fairly primitive mammal. Here both cerebral hemisphere and cerebellum are well developed, and the former has grown backwards and covers the mid-brain completely so that it cannot be seen from the side. This growth has largely taken place in the roof of the fore-brain. From a brain like this the human brain can be derived by imagining this growth of the cerebral hemispheres greatly exaggerated, and their surface becoming wrinkled to increase the area of the now essential cortex. As a complicating factor man walks upright, so his brain is twisted in such a way that the spinal cord runs downwards from it instead of coming straight out behind.

How does this structural divergence between the brains of reptiles and birds on the one hand and mammals on the other reflect itself in their behaviour?

The outstanding difference between mammals and other vertebrates lies in the adaptability of the former. They can remember more surely and learn more quickly than any other living things. Moreover, they tackle a new problem more competently. Suppose you put a fish, or a frog, or a reptile, in some experimentally devised strange situation—such as a maze in which the animal has to follow a definite path if it is to reach a comfortable nest and food, while other possible paths lead nowhere. It will simply muddle about among the unfamiliar surroundings until it gets to the goal. Put the animal in again, and it will muddle its way through again; but gradually, as the lessons are repeated, it will get less and less dilatory and make with more and more directness and certainty for the goal. This kind of learning is simply trial-and-error, like the random trial-and-error of a slipper

animalcule, but with a certain element of memory attached to it.

Yerkes, an American investigator, devised a maze for some tortoises on which he was experimenting. Part of the path to the comfortable nest, to which they were supposed to find their way, led down a steep inclined plane. It so happened that one of the tortoises, put in the maze and not liking the look of it overmuch, began poking aimlessly about and tumbled off the side of the sloping plane. Surprisingly, it found itself near a pleasant nest. Thereafter this animal invariably solved the problem by repeating his accident—by making for the edge of the plane, deliberately tumbling over, and then calmly walking into the nest.

To a large extent, all animals learn in this way—by muddling about more or less at random, and by remembering which activities are followed by pleasing results and which by harmful. But mammals do it very much more quickly and less laboriously than other vertebrates. Moreover, in the higher mammals at any rate there often appears a somewhat different kind of solution when the animal comes up against anything new. The creature supplements this profiting by chance events by means of inner resources of its own. It stops to think ; then it " gets an idea " ; then it tries the new idea to see whether it will work.

How far this reflective pause is really a process that differs in kind from the simpler learning, and how far it is merely an extension of that process made possible by the greater extent and better organization of the store-rooms of the mammal's memory—an overhauling of past experience to find whether there is any illuminating precedent—is a question that will come up for review in a later section, when the intelligence of mammals will receive a more thorough examination. Here it is enough to note, as a fact of observation, that mammals are altogether more competent to deal with novel and puzzling situations than any other vertebrates.

A mammal—or at any rate a higher mammal—thinks by means of its cerebral cortex. In ourselves, everything that is

not simply automatic is determined from that dominating centre. But this does not mean that learning is always confined to the cortex. Indeed, in frogs and fishes this structure is absent, and yet a certain slow learning is possible, although their adaptability is slight compared with our own. Their somewhat rudimentary counterparts of our higher mental processes are apparently performed mainly by the thalamus and other incipient correlation centres; perhaps in some cases by the mid-brain also. The growth of the cerebral cortex represents an extension and elaboration of this ability. Cortical tissue is grey matter arranged in such a way that it can do these things much more effectively. There is evidence that the power of the thalamus to participate in the formation of habits persists in birds. But in mammals the chief mental processes are carried out by the cortex.

The evolution of the mammalian brain is largely a matter of the improvement of this all-important grey film of tissue. It increases in comparative size and comes to overlap more and more of the other regions of the brain, until in ourselves only the cerebral cortex and the cerebellum are visible from the side, and only the first from above. At the same time it increases greatly in complication. As in the early mammals the new centre began to prove its worth, the older brain regions became more and more subservient to it. Its fibrous connections thickened enormously as it grew, and it took over more and more of the responsibility of running the body state.

Here let us note the meaning of two further words which are making their way into popular biological writing. The cortex of a tortoise—the most primitive cortex we know—is divisible into three distinct fields. At the outside and inside edges of the roof of each hemisphere it is supplied chiefly with fibres from the edges of the corpus striatum below. The information supplied to these lower regions, and through them to the marginal field of the cortex, is mainly concerned with smell, taste, and the condition of the viscera. But the third strip of cortex, lying along the middle

of the roof of the hemispheres, is mainly connected with the thalami in the side walls of the between-brain, and thus indirectly receives information from the eyes, the ears, the skin, and the tendons, joints, and muscles involved in position and voluntary movement. Naturally these three regions do not work in isolation, but as a single unit. Nevertheless, all through the mammalian series, it is possible to make out a similar distinction between the parts of the cortex which are mainly concerned with smell and taste and the parts mainly concerned with sight, hearing and touch. But their importance varies. The part concerned with smell and taste is well developed in the most primitive mammals; it was the first of the two to assume its definitive elaborate form, and is known as the *archipallium*. The other part is small in primitive mammals, but acquires more and more relative importance, until in ourselves it is enormously expanded and overshadows the archipallium completely. This part is called the *neopallium*. The shift of responsibility from archipallium to neopallium corresponds to a gradual alteration in behaviour, to the shrinking of the nose and the improvement of the eyes and (since the neopallial tissue is differently and more efficiently disposed than the archipallial) to an increase of intelligence and adaptability.

Thus the mammalian brain has evolved. The primitive amphibians are spawned in great multitudes; they are stupid, inadaptable creatures, but out of the thousands thus launched a few survive to carry on the species. The higher mammals reproduce altogether more sparingly, but they are better able to take care of themselves and to survive unusual combinations of circumstances. A large share of the responsibility for carrying on the race has been handed from the genital organs to the brain, from the proliferating germ-plasm to the thinking individual soma. But meanwhile the other vertebrate line that leads up to the birds took a somewhat different direction.

Birds can learn. Anybody who has seen performing pigeons in a music-hall knows that their brains can hold one

or two tricks. But performing pigeons generally come on the stage in great flocks, for the number of tricks that any single bird can do is much less than the repertoire of a good performing mammal. There are, it is true, some directions in which a bird can learn rapidly. Newly hatched chicks, for instance, at first peck indiscriminately at any small objects within range—grains of corn, caterpillars, ink-marks on paper, their own feet, or their fellows' eyes; but they soon learn to disregard what is useless as food, and it only requires one or two repetitions of the unpleasant experience of some bitter-tasting caterpillar to teach them to avoid caterpillars of that kind in future. Thus while instinct lays down for an insect what kind of food it is to eat, a bird's instinct only tells it to try all kinds of food; and it depends upon its power of learning to find what is good and what bad. In this particular direction birds learn very rapidly, and the biological value of this is obvious; but in most other directions they only seem to learn very slowly, and if the task to be learnt is at all complicated they are often unable to master it at all. In maze-learning, for instance, birds show up very badly. Indeed, the educability of a bird is hardly greater than the educability of a reptile, and certainly less than that of a rat. Where birds excel is in the performance of elaborate but purely instinctive acts. An incubator-hatched bird will build its nest as neatly and pick its material as carefully as any other member of its species; at the first appropriate occasion it will go through the routine of courtship with perfect correctness. In a word, the great development of the corpus striatum in birds means a tremendous endowment of inherited instinct, rivalling that of insects in its complexity and far exceeding our own, but without any notable individual intelligence or adaptability to modulate it.

Often the instinctive behaviour of a bird is not perfect when it first appears. For the first few days after hatching a chick will often miss a grain of corn at which it pecks, while this will seldom happen with a week-old bird. The improvement is partly due to practice; but that it is not

altogether so can be shown by keeping the chicks for some days in the dark, so that they can see nothing to peck at, feeding them occasionally by hand. Yet when they are let out it is found that they very soon catch up in their accuracy of pecking with other chicks of the same age. The mechanism of the pecking reaction has grown more accurate without being used. The development of instinctive behaviour in this way, by spontaneous growth rather than by practice, is known as *maturation.* We do not know how much of maturation is due to growth of the sense-organs, how much to growth of the muscles, and how much to growth of the brain. All that we can say at present is that some part of the mechanism has grown more perfect. Another example of improvement in instinctive behaviour which is largely due to maturation is found in the early efforts of young birds to fly. In the same way the improvement in a puppy's efforts to walk, and in various activities of human babies, is partly due to maturation; but in the development of mammalian behaviour a greater part is played by learning and a smaller part by maturation than in birds.

An admirable example of blindly mechanical instinct is afforded by the so-called thermometer bird or brush turkey of the Solomon Islands. The eggs in this species are laid in heaps of mixed plant material and sand, and incubated for some six weeks by the heat of the rotting vegetable matter. Moreover, they all lie with the blunt end upwards. The chicks hatch out from this blunt end, and their feathers all point stiffly backwards; so by wriggling and struggling in the heap they can force their way upwards. As soon as they get out they shake themselves, and then dash into the shadow of the nearest undergrowth. Here we have an admirably adaptive chain of reactions. But if you take a chick which has just liberated itself and dig it into the heap again, it is quite incapable of coming out once more, but stays there struggling ineffectively until it dies. Its movements are now of the wrong kind. The reactions follow one another automatically, a mechanical chain of instinct, and the creature

can no more go back to the beginning and start again than can the cocoon-spinning caterpillars described in Chapter II, § 3.

One of the present authors (J. S. H.) has given another illustration in his *Essays of a Biologist* of how limited the behaviour of a bird may appear when some unforeseen accident disturbs the usual routine of its instinctive acts. The scene described has been filmed by Mr. Chance, and the chief actor is a pipit in whose nest a cuckoo has laid her egg.

When, after prodigious exertions, the unfledged cuckoo has ejected its foster-brothers and sisters from their home, it sometimes happens that one of them is caught on or close to the rim of the nest. One such case was recorded by Mr. Chance's camera. The unfortunate fledgeling scrambled about on the branches below the nest; the parent pipit flew back with food; the cries and open mouth of the ejected bird attracted attention and it was fed; and the mother then settled down upon the nest as if all was in normal order. Meanwhile, the movements of the fledgeling in the foreground grew feebler, and one could imagine its voice quavering off, fainter and fainter, as its vital warmth departed. At the next return of the parent with food the young one was dead.

It was the utter stupidity of the mother that was so impressive—its simple response to stimulus—of feeding to the stimulus of the young's cry and open mouth, of brooding to that of the nest with something warm and feathery contained in it—its neglect of any steps whatsoever to restore the fallen nestling to safety.

Clearly we are dealing here with a far more mechanical type of conduct than occurs when the mammalian cortex is at work. One cannot imagine anything to parallel this in the behaviour of a bitch or a ewe.

§ 5

Courtship in Animals

On a fine spring day go to the Zoo and stand in front of the Amherst pheasants' cage. The hen is a dowdy creature; her dowdiness is protective. But the male is brilliant in the extreme, with his fabulous colours, gorgeous tail and frill.

If you are lucky, you will see him go through his courtship. He makes a little rush past the hen; as he passes, he droops his wing, shows off his tail and fans forward the frill on his head. Then he will repeat the process from the other direction. You are struck by the way in which the display is directed at the female. It is only executed at the moment of the rush past, the body and the tail are sloped towards the hen, and only on the one side is the frill fanned out. The frill on the far side is kept closed; he wastes no beauties where they will not be seen.

Most people have seen a peacock displaying his train—perhaps the most sheerly beautiful sight in nature. The bustard inflates his throat, throws back his head, and everts his wings so that he may strut before the hen, like a surprising animated giant white chrysanthemum. The Argus pheasant is perhaps the most striking of all. The long brown wings, patterned with a series of light spots, wonderfully shaded so that they look like solid spheres, are spread and thrown forwards like the bell of a great flower. The long tail plumes are waved up and down behind, and from below one wing an eye peeps out to keep the hen in view.

Here we have in its fullest development the phenomenon of "courtship" which plays a large part in the life of a great number of the higher animals. It is not confined to the vertebrates. The lowest types in which the process can be traced are certain marine bristle-worms. At the breeding season, the males may be seen writhing and contorting themselves in a frenzied dance among the females; this appears to stimulate the females to shed their eggs, whereupon the males emit their sperms. The masculine excitement has been turned into a stimulus for the females' egg-discharging instincts.

In the alert and half-terrestrial fiddler-crabs there is a rudimentary but illuminating form of display. The females have two small claws, with which they feed. The males have to be content with one feeding-claw, for the other claw is huge, sometimes nearly as big as the rest of the animal, and in some species brightly coloured. When, in the mating

season, a female crab appears, the males in her path stand tiptoe, with their single huge claw held aloft —a statuesque attitude. If she is indifferent, they may run along a little and strike their attitude again, but will not pursue her far. As Dr. Pearse writes, after watching them carefully, " they seem to be advertising their maleness." There you have the clue. There are not many possible situations in a fiddler-crab's life. There are food-situations, danger-situations, and sexual-situations. The male's upreaching pose, with his masculine appendage so prominently displayed, is an advertisement to the female that a sexual-situation exists, and so is not only an advertisement, but a potential stimulus.

Similar excitation occurs in the case of snails, octopuses, and cuttle-fish, but good studies of these processes have still to be made.

This apprising the female of the existence of a sexual-situation is of vital importance in many spiders. Here a smallish moving object is normally the sign of a food-situation—a stimulus for the female to pounce and kill. Accordingly it becomes essential for the male to distinguish himself sharply from other smallish moving objects. Among the almost blind web-spinning spiders, he does this by approaching the web and vibrating one strand, producing a movement quite different from that due to the struggles of captured prey. The female may rush at him once or twice (on which he very hastily makes himself scarce), but eventually this message of love vibrating along the web attunes her to the sexual situation. Even so, however, after mating has been accomplished, he may again become a mere moving object to her, and she may then kill and eat him.

In scorpions, Fabre has described a sort of set-to-partners of courting male and female; but here it seems to be the invariable rule for the female, once one instinct is satisfied, to change to another, and eat the male after his biological duty to the race has been carried out. And the female of the predaceous praying mantis may begin eating her mate while the act is still being accomplished.

The instrumental music of the grasshoppers and crickets (leg on leg, or wing-case on wing-case) serves a sexual function, but it is rather one of bringing the sexes together than of courtship; and the same holds for the flashing of fireflies and the glowing of glow-worms. But the little carnivorous flies called Empids have a true and very interesting courtship.

In some species, the males present the females with insect prey which they have captured; and usually the gift is either wrapped in silk spun by the male or embedded in a large glistering " balloon " of bubbles which he has secreted, as the gift of a necklace might be enclosed in a striking casket. Carrying these embellished gifts in their legs, they fly to and fro over pools and streams. Here the mere advertisement of a sex-situation is reinforced by the stimulus of a gift. But in other species, the place of the prey is taken by a flower petal or a blade of grass, and the males will put coloured paper in their balloons if you strew it for them; this appears to be the only case outside warm-blooded vertebrates in which objects are picked up and used in courtship for what we may call their æsthetic appeal.

Many female insects cannot ripen their eggs without a rich protein meal; the female mosquito, for instance, needs blood. This may account for the female mantis or spider devouring her mate; and so the gift of prey may save the male Empid's life.

Throughout the vertebrates there is a steady development of this business of courtship. In fish it is exceptional, and is found mostly where internal fertilization is necessary. But where it does occur, it may be quite elaborate. The male dragonet assumes the most brilliant colouring in the breeding season, and flutters round the female like a gorgeous butterfly. The little sword-tails owe their name to the male's long-bladed tail fin, with which he prods and pokes the female into interest as he swims about her. And in the humble stickleback of country ponds, the male becomes a lovely iridescent creature in the spring, bright with rich red, which kindles

with his excitement or pales if he is beaten and chased away by a rival.

Among amphibians there is a marked difference between the courtship of the tailless frogs and toads and the tailed newts and salamanders, a difference connected with their methods of reproduction. In the frogs and toads, the male waits, tightly clasping the female, until she lays her eggs, when he ejects his sperm upon them. There is thus no need of courtship, but only of the sexes finding each other, and accordingly the spring behaviour of the males is limited to vocal performances which advertise their whereabouts. But, as we have described in §3, the fertilization of most newts and their allies is more elaborate. It is necessary that the female should be roused to play her part. To this end the male newts have a magnificent nuptial dress and courtship-dance, in which with arched back they prance in front of the female, while the tail wafts the presumably odorous secretion of certain glands towards her. And it has been proved by experiment that she will not pick up a sperm-packet unless a courting male is about—in the absence of such stimulation she treats it with complete indifference.

The courtship of reptiles has been comparatively little investigated. Among our fragmentary knowledge about them is the fact that various snakes, including the common European grass-snake, will assemble in writhing, intertwined masses in the spring, apparently for the purpose of choosing mates; and that the males of some of the Australian lizards will get up on their hind legs and wrestle in the most human-looking way for the possession of the female. The most careful studies have been made by G. K. Noble on various lizards. Here it seems that the bright colours frequently seen in the males have no significance in impressing the females, but serve as warnings to other males which come too close. As with the rattlesnake's rattle, the warning is aimed at preventing an encounter which, though it might end badly for the other party, yet might also damage or exhaust the owner of the warning character. The difference

is that the rattlesnake's rattle is a warning directed against enemies of other species, while the lizards' colours and attitudes are threats directed against rivals of the same sex or species. In some lizards the display of the bright colour and the puffing up of the body to appear larger than it really is, seem never to be followed by actual fighting. The threat has become mere bluff—yet the bluff works.

It is in birds that courtship-display reaches its greatest elaboration. We will begin with some account of the usual type of courtship in song-birds, which Eliot Howard has observed with such patience and analysed with such care in his *Territory in Bird Life*.

In migratory song-birds, such as the Old World warblers, the males in spring arrive at their breeding quarters a week or so ahead of the females. They then proceed to find suitable sites for nesting, and each appropriates a more or less definite area or territory for himself. He may have to fight to obtain it, and is almost sure to have to fight to keep it. There he awaits the arrival of the hens, spending in song almost all the time left over from feeding and sleeping. When the hen-birds arrive, they search for the songsters. One may simply take possession of a male and a home without any ado. Or she may have to fight another hen for her prizes; in such a quarrel the male, though often an interested spectator, will not take sides, and becomes the associate of the victress. There appears to be no courtship-display on his part at this juncture, although from this moment onwards the pair are mated.

The prominent colours and striking songs of the males seem during this period to be primarily threats to potential rivals not to invade the bird's territory on pain of a fight, though the songs undoubtedly serve also as an advertisement to potential mates—an advertisement of a home and husband.

Most small birds, it seems, are mated for the duration of one brood only. For though many birds, like storks and parrots, eagles and ravens, do mate in permanency, the recent practice of bird-banding, by which wild birds are temporarily

trapped and have light metal identification rings fastened round their legs, has revealed an unexpected inconstancy in the marriage systems of small song-birds. The most systematic study has been made on an American wren. Mr. Baldwin had a large number of pairs of wrens occupying nest-boxes in his orchard. During their first brood of the season he banded all of them. Then while the second brood was being raised, he caught the birds again, and found to his surprise that the great majority had changed partners between broods! The single brood or the single season appears to be the usual time for which song-bird matings last; but during this period the marriage is definite and monogamous.

It is after the mating that the males begin their display. They have yet to excite the female to actual intercourse. It is to that end that most courtship is directed. Although the warblers are mostly very soberly coloured, they display as many gaudy birds do—they spread their wings, fan their tails, bristle up the feathers on throat and head. At the same time they often seize on some piece of potential nest-material, such as twig or leaf, and advance towards the female with it in their mouths. There seems to be a strong association in their minds between the two emotionally-coloured activities of courtship and of nest-building. In addition, a frequent form of courtship is the pursuit-flight, in which the cock darts, twisting and turning, after his mate. The hen warbler may be interested in the male and his displays, but it is not until after an "engagement period" of a few days that she permits the consummation of their mating; and shortly after this the first egg is laid. The hen in most song-birds does all or the greater part of the work of brooding the eggs. But once the eggs hatch, both parents share in collecting enough food for the prodigiously rapid growth of the fledgelings.

In song-birds that are not migratory, but resident all the year round (as in the buntings studied by Howard), the males often begin to stake out their territorial claims in

January or February, spending an increasing part of each day on their territory as individualists, a decreasing time with the flock as gregarious creatures. The females leave the flock and follow them on to the territories a few weeks later, but still much earlier than the beginning of egg-laying; so that the "engagement period" is here very much prolonged.

The "engagement period" probably has a physiological basis. We know that in pigeons at least there are two stages in the growth of the eggs in the ovary. At first, yolk is laid on very slowly; but a few days before the egg is ready the rapidity of yolk-growth suddenly increases about twentyfold. And this change is associated with profound alterations in bodily chemistry; the amount of sugar in the blood increases, the adrenals enlarge, and other ductless glands alter their activities. It is probable that the end of the "engagement period" coincides with this change in female metabolism. In any case, while the males have but two main phases in their sexual life—unsexed in winter, fully-sexed in the breeding season—the females have three; they pass from winter neutrality to full breeding activity through a third, intermediate phase, in which they are enough sexed to take an interest in their territories and future mates, but not sufficiently so to be ready to pair. The familiar and rather ludicrous spectacle of a cock sparrow hopping lovesick before a hen who repels his advances by violent peckings is due to the hen being only in the half-way stage, while he is fully ardent. Often not one but many male sparrows will gather in fruitless and disorderly courtship round one hen. In such cases the sight of one bird courting has excited the rest. The same spread of excitements at the sight of display (or of combat) may be witnessed in other birds; but in the sociable sparrow, with his dense urban population, it is more frequent and leads to bigger gatherings.

The biological function of display seems to be the emotional stimulation of the female; display prompts to the

act of mating rather than to the choice of marriage partner. This is demonstrably so in newts. Even if two rival male newts deposited their sperm-packets before a single female and simultaneously executed a courtship dance, it would be asking too much of amphibian mind to suppose that she would remember which packet belonged to which male, and would pick up the packet deposited by the one whose dance pleased or excited her most.

Where we should expect male competition and sexual selection to have fullest scope is in species that, like the Ruff, are polygamous, or promiscuous in their mating habits, so that each female has the choice between many males. The facts confirm our expectations. Edmund Selous spent a whole spring watching a ruff assembly-place in Holland. In spring the males repair to definite areas called "hills," since they are generally a few feet above the marsh. On one such hill there may be anything from half a dozen to twenty or thirty males. They whirl round like dancing dervishes in sheer overwhelming excitement, or spar viciously with each other. Occasionally the females, or reeves, visit the hill, and it is there that actual pairing occurs. This is the only contact between the male and female, for the males never visit the nests or look after the young.

When a reeve visits the hill the scene changes. The ruffs squat or prostrate themselves in strange attitudes—wings spread out, beak pointing down at the ground. They will remain thus, as if hypnotized, for a considerable time, occasionally shifting round to face in a new direction. Sometimes the reeve will just fly away again; sometimes she will walk up to one of the ruffs and touch him with her bill, on which mating will take place. The choice lies entirely with her.

Selous soon distinguished all the male frequenters of his particular hill, for the ruff is a unique animal in its variability, every male differing from every other in the details of its breeding dress; and he found that their success in

obtaining mates was very unequal. One bird (interestingly enough, one whose appearance was to human eyes very striking) mated more often than all the other males on the hill put together; and there were several males who never mated at all. Here is Darwin's sexual selection in diagrammatic form. The females can be seen exercising a choice of mates, and some males are chosen much more frequently than others; and so some have many offspring, some few, some none. The premium upon whatever promotes feminine choice is therefore much higher than where monogamy prevails, and, accordingly, we find that the polygamous birds usually have more elaborate display-characters than their congeners.

It is harder to understand the biological value of courtship-display in monogamous creatures like song-birds. However, as Eliot Howard has shown us, display undoubtedly helps to regulate the emotional reactions of the pair, and so ensures that both male and female shall at intervals be brought simultaneously into a state of readiness to pair. Female doves reared in solitary captivity can be made to lay eggs (though the eggs will, of course, be infertile) by keeping them in the next cage to a male; the emotional stimulus of his bowings and scrapings will set going some change in their ductless glands which will lead to egg-production. Even caressing a virgin pigeon's head with the finger, so imitating the billings of the male, may have the same result.

In creatures like grebes, where courtship is a joint affair of the two sexes, the stimulation is doubtless mutual. But here it looks as if other functions had been added on. No one who has watched grebes, or other birds with elaborate mutual courtship ceremonies, can doubt that their performance is extremely pleasurable; and in all these kinds of birds the ceremonies continue right through the season, from the moment of pairing-up until the young are well-grown. And both parents must share the duties of incubating the eggs and feeding the young if the full complement

of offspring is to be reared. It looks as if the elaborate display-ceremonies constituted an emotional bond between the pair, which, by helping to keep them together through the season, cemented a union which was of biological value. This is no fantastic suggestion, for something of the same sort is obviously at work in human family life.

This brings us to the relation between kind of courtship and way of life. Courtship and display in general are seen to have as their main function the stimulation of the other sex's emotions. But the means by which courtship achieves this end differs according to the habits of the species. Need for protection through inconspicuousness will work against the tendency of sexual selection to produce brilliant colours and striking display ornaments. Where sexual selection is very strong, as when polygamy is the rule, extra weight is put into the scale against this need for protection, and we get the fantastic beauties of the male pea-fowl, ruff, or black-game. But when monogamy is practised, and the birds are in danger from hawks and other enemies, sexual selection is weaker, the need for protection greater; and so we have the state of affairs seen in larks or Old World warblers, or the common European quail and partridge, in which the male is almost as dull-coloured as the female, and courtship consists merely of exciting actions.

Often a compromise is struck between the exigencies of sexual and natural selection by having the bright colours tucked away out of sight during ordinary existence, but brought suddenly into play at courtship. The great bustard is an excellent example of this, and so is the prairie hen, where the males during courtship ruffle up tufts of feathers on either side of their neck, and so reveal brilliant patches of bare skin which they then inflate into the semblance of half-oranges. Such displays have as additional advantage the stimulus of novelty and strangeness.

Birds which have few or no enemies to fear, such as the gregariously-nesting herons and spoonbills, are often very conspicuous—snow-white, for instance—since there is no

special need for protection, while the conspicuous colour helps the birds to recognize each other from far off.

Courtship is also subtly entangled with family life. In almost all song-birds the food-territory round the nest is the basis of reproductive success. And the fights of such birds are concerned with property rights rather than with sex. Male fights male to secure territory; female fights female to secure a male—but only if he is already in possession of a territory; and pair fights pair over boundary disputes. Song is also in the main concerned with territory. When at its most intense it is serving a double territorial purpose. It is an advertisement to any female within hearing that here is a male in possession of an eligible nesting-site; and it is a warning notice to other males—trespassers keep out, or else fight.

Song being thus essentially an advertisement, is generally given from as conspicuous a position as is consonant with safety. Where there are trees most birds sing from a top branch; where there are none, the singers often make up for their absence by aerial songs—as larks over fields and heaths, or pipits over moors. Many wading-birds, too, have songs or their equivalents, and they also give them aerially; we have only to think of redshank or curlew or godwit. In snipe, the aerial "song" is mechanically produced; the strange, far-carrying bleat is made by air vibrating the spread tail-feathers. Many woodpeckers also have a mechanical substitute for song; they drum their beaks with incredible rapidity on dead branches to make a resonant note; and some, like the American red-headed woodpecker, select their instrument, making trial of tin roofs, the metal arms of telephone insulators and so forth, until they find something to their liking. Ruffs and such-like birds have no territory, and therefore no song.

To say that song is a territorial advertisement does not imply that it is never given save with some territorial meaning. Nature does not work in that way; she employs machinery which ensures that on the whole the biological

functions of song shall be carried out, but does not worry if the bird sings on other occasions too. Male birds are constructed so that they shall sing when in certain physiological states. For most song-birds, one condition is that the gonad shall be pouring its hormone into the blood; another is that they shall enjoy a sense of well-being and not be cold or starved. A third is that they shall not have additional calls upon them. Almost all male song-birds stop singing when the eggs hatch, and they have to begin foraging for their young; but if now the young are destroyed, song will begin again almost at once. When family cares are past, and moulting is over, many birds have a period of autumnal song before their gonads shrink and turn them into neuters again for the winter.

Similarly, the sex activities of ruffs or black-cock depend primarily upon sex-hormones and superabundant vigour. The males will continue dancing and sparring on their assembly-places for weeks after all the hens, now fully occupied with their eggs and young, have ceased to visit them. Some observers have for this reason concluded that the assemblages can have nothing to do with sexual selection; but this is to misunderstand the blind and blundering way in which selection works.

We often find even the details of display determined by the bird's mode of living. Diving-birds may use their powers to disappear below the surface and re-emerge close to their mate in what must assuredly be an aggreeably stimulating manner; this occurs in the grebe and some diving ducks. Or they may raise fountains of spray with their feet, as does the golden-eye duck, or rush erect over the water, in apparent defiance of the laws of hydrostatics, like the loon. Birds that are masters of flight use air as their medium; the peregrine tiercel will dash down-wind at the falcon as she sits on a rocky ledge, and swerve up when only a foot or two from her. The crepuscular insect-hawking nightjar of Europe flies moth-like above his mate, and now and again claps his wings startlingly above his

back; an African species trails strange whip-like plumes in his display-flight; the related American bull-bat lets himself drop from hundreds of feet aloft, and swerves up with a "zoom."

Fulmar petrels have no bright colours of plumage; but for their display they use "interior decoration," in the shape of the delicate mauve lining of their mouths; two fulmars languishingly waving their open mouths at each other is a sight not to be forgotten. Male Adelie penguins present their mates with nesting material—in this case stones—and the pair indulge in a mutual ceremony which Dr. Levick, in his delightful book *Antarctic Penguins*, calls "going into the ecstatic attitude." Mutuality in courtship and display was hardly known in Darwin's time, but is actually quite common. We find it not only in herons, grebes, petrels, penguins, but also in divers and pelicans, in cranes and terns, in the dull-coloured stone-curlew, and in the flightless but well-crested kagu, and in the great albatrosses of the Laysan Islands.

The males of the bower-birds, an Australian group, construct peculiar bowers which are quite different from the nests. The bower often consists of a short tunnel of twigs, at the entrance to which the bird deposits shells, bones, berries and other bright objects, different species showing preferences for different colours. This museum of specimens appears to be a substitute for courtship decorations, and the "display" of the male consists in his driving the female through the bower and drawing her attention to his collection. In another species there is no actual bower, but the male clears a space a few feet across, and on it lays a certain kind of leaf with silvery under-side. He always puts the leaf with its silvery side showing, and if the wind blows it over, turns it right way up again. As the leaves wither, he clears them away and brings new ones

The small lobe-footed waders known as Phalaropes afford another interesting case. The females are rather larger and more brilliantly coloured, and the whole duty of

incubation and feeding the young devolves upon the males. In courtship, too, it appears that the females take the more active part. Sexual selection has here been reversed.

Sometimes, instead of presenting nest-building material to his mate, the male bird may present food. The male harrier, returned from his hunting, gives a special call when near the nest; the female leaves her eggs and flies below him. At the right moment he drops his prey; she, back-somersaulting almost completely, catches it in her claws, and returns to her duties. Male terns give their mates fish, male titmice present theirs with caterpillars. In many such cases the female while being fed adopts the same attitude and gives the same call as does the half-grown young when begging food from its parents—a simple example of association. More subtle is the cross-association with sex, which may be witnessed in various birds, notably the common house-sparrow, where this same attitude and note is used by the female as a symbol of readiness to pair.

Psychologists, indeed, have in the courtship-behaviour of birds a rich field to explore. We have already mentioned the association between the presentation of nest-material and courtship-ceremonies. A good example of the transference of this attention to an unusual object is found in the Adelie penguin. When there are men near their rookeries, these brave but comic little creatures will sometimes approach them instead of their mates, and solemnly deposit a stone at their feet. Dr. Levick records that he was quite embarrassed the first time that he was a recipient of this tender attention. They may also make these gifts to sledge-dogs; but then matters may end disastrously, for the dog will often snap at them and kill them. It would appear that this action is an expression of special interest. The only way in which it can be normally expressed is to a bird of opposite sex; but strange, impressive beings provide fresh outlets.

Another queer transference of instinct, recalling certain traits of abnormal human behaviour, was noted in a male

argus pheasant in the Amsterdam Zoo. As no mate of its own kind was available, the bird was put with a female of a related species. Now in the courtship of the ordinary argus pheasant the hen usually stands and looks on while the male shows off his plumes. But matters must be different in the species to which this hen belonged, for she absolutely refused to stay still. The male grew more and more discouraged. He rushed about the cage, throwing up his wings and tail spectacularly; but when he peeped under his wing, the hen had moved on. Eventually he gave it up; but the urge to display was still on him, and he indulged it by performing before the dish in which his food was put out! The dish might be inanimate, but at least it was associated with some form of gratification.

In mammals courtship is less frequent and, when present, less spectacular than in birds. Often, as in deer and wild sheep, bisons and sea-lions, there is no courtship, but the males fight for the possession of the females, who passively fall to the lot of the victor. Such males are naturally characterized by weapons and prowess in fighting, and display-decorations are absent.

Deer size each other up from afar, and battle is not joined unless the rivals are on fairly equal terms; for each encounter that comes to fighting, there are a dozen where one beast slips away. But once the fight has begun, it is fierce; the combatants shove with antlers interlocked, and whichever gives up first has to beware lest, as he disengages, the other's brow-tine pierce his neck. The break-away is thus the most exciting moment of a fight; the vanquished unlocks his antlers and is round and away in a flash.

In sea-lions and sea-elephants, the bulls, who are generally enormously bigger and stronger than the cows, come ashore on the breeding-beaches and stake out mating-territories there. As the females land, the males fight for them and establish harems. In some species they may seize the cows by the neck and pitch them over their shoulders into the harem. The old bulls are so busy defending their sexual

rights that they take no food at all during the breeding season, which lasts for several weeks. In spite of this, their vigilance is sometimes deceived; in one species at least the cows may occasionally slip off into the sea, and there mate with the half-grown bulls who are too small to fight and establish harems of their own. But doubtless the official husband hands on his genes in a sufficiency of cases to make strength and valour pay in the struggle for reproduction.

However, in many mammals there is little of either fighting or display in connection with sex. In dogs, for instance, the male is only attracted by the female when she is ready to receive him; and at such times her scent stimulates all the dogs within a mile. The reproduction of most mammals, indeed, is on a more physiological, less psychological plane than that of most birds. Emotional stimulation has no influence upon the development of their eggs, but an automatic cycle of the ductless glands controls the female's mating rhythm. The sexual situation is brought into being from within and so needs no stimulus from without. In polygamous mammals, capture of females is enough. When the time comes, they will accept the victor. And in monogamous species, some apprisal (usually by scent) of the female's physiological state is often sufficient.

Matters are not always quite so simple as this; there are many cases on record of female mammals—mares or bitches, for instance—who refused to have anything to do with particular males; and it is probable that careful observation would reveal many examples of discrimination. But the broad fact remains that in mammals, as compared with birds, courtship is rare, and display rudimentary; and the explanation undoubtedly is to be sought in the difference in their reproductive physiology.

The monkeys and apes alone among mammals have begun to subordinate the chemical control of reproduction to a control by the higher centres of the brain. The fish or amphibian, reptile or bird, has a fixed breeding season. At other times of the year it is indeed, physiologically speaking,

castrated; its ovary or testis shrinks to a tiny fraction of its breeding size, and the amount of sex-hormone in the blood falls until it has no effect. The creature oscillates each year between two phases of existence, a neutral and a sexual being. Most female mammals, in addition to the annual cycle of breeding season and neuter season, have a cycle within the breeding season, of readiness to mate and the reverse, determined by the state of the eggs in the ovary. But in monkeys and apes not only will the females mate at other times of this ovarian cycle, but the neuter part of the annual cycle also shrinks. Some human races (like the Eskimos) conserve traces of a restricted breeding season, but in civilized man it has disappeared. In the higher primates, the chemical control of mating is only slight, the emotional control predominant.

And parallel with this change, secondary sexual characters come into prominence, although never so strikingly as in birds. Many male monkeys have facial trappings, sometimes bizarre to human eyes, sometimes alarmingly reminiscent of human whiskers or moustachios. These, however seem to be rather threat-characters for use against rivals than display-characters for the stimulation of mates. The males of baboons and their relatives have bright-coloured posteriors—pink in the baboons, blue-and-red in the Mandrill and Drill; but the meaning of these is unknown. However, practically all female monkeys and apes have a naked patch of pink or red skin behind, which swells at certain seasons; and the function of this seems definitely to be to attract the males—it is a symbol of readiness to mate. The abandonment of this posterior display was a very important step in human ancestry; for it meant that interest could be chiefly concentrated on the face, and features and expression could become the main appeal of love.

In man, the predominance of mind has allowed a more deliberate choice of mates; and with this, courtship enters on a new phase. Feminine beauty becomes, almost for the first time in the history of life, more important than

masculine decoration. Dress and finery, gifts and poems, can excite in the place of special plumage or inborn colours. Physical prowess, brains, wealth, can all become linked up with courtship. Sex and mating cease to be in a compartment of life by themselves; it is a prime characteristic of human mind that it enables different aspects of existence to be brought into relation with each other, different departments of life to interpenetrate.

The varied and individualized love-making of humanity differs fundamentally from the courtship of birds. The human lover woos with the cerebral cortex, he (or she) is plastic and responsive, and adapts the means to the occasion. The impassioned bird woos ardently but automatically with the corpus striatum. In one case the individual of the opposite sex is a problem; in the other an exciting situation. The human lover may do a thousand things; the courting bird is an elegant determinate machine.

§ 6

The Evolution of Mammalian Intelligence

The intelligent mind is a mammalian invention; compared with any of the higher mammals, a bird is little more than a highly complicated and highly emotional instinctive machine. But before we turn to a fuller analysis of the growth and meaning of intelligence, let us warn ourselves against the tendency to exaggerate this contrast unduly and to overrate the mental powers of mammals because of their many other resemblances to ourselves. As a matter of fact, the reputation of mammals in this respect has sunk considerably during the past half-century. Nowhere has the rigour of the scientific attitude of mind been more destructive of loose and tolerant ideas than in this field. Fifty years ago, books on animal psychology were largely occupied with the mammals, and nearly all that space was taken up by anecdotes illustrating their wisdom. We are all familiar with

the elephant who cherished a grudge and squirted his old enemy with dirty water after thirty years; or with the lion who refused to eat his benefactor Androcles. We have all been assured of the exceptional cleverness of our neighbour's dog or cat. The laws that govern social intercourse have perhaps forbidden any explicit expression of disbelief in these marvels; yet, inwardly, a certain saving scepticism has reminded us that anecdotal evidence is often untrustworthy. For one thing, it picks on occasional striking events for narration, and, for all we know, they may be accidents or coincidences; for another, it usually depends on the report of a casual observer, untrained in what to look for and prone to read his own private ideas and interpretations into what he sees.

So let us go into this matter of mammalian intelligence with care and circumspection; and let the reader beware of too hasty indignation if in what follows we seem to be disrespectful towards some particular four-footed favourite of his or her own.

The lower of the two main branches of the mammalian stock, the marsupials, are on the whole stupid creatures, above the reptiles in respect of their warm blood and their mode of reproduction, but hardly in their behaviour. They seem to learn with difficulty, and this is helping towards their extermination in Australia; they are no match for the more enterprising and plastic placentals introduced by man. The few marsupial carnivores, such as Tasmanian devil and marsupial wolf, are almost untameable. They are fierce bits of flesh-eating machinery that go their way almost regardless of change in outer circumstance. In zoos, for instance, they do not get to know their keepers in the personal and intimate way of lions or wolves or seals. The placental wolf has been tamed into our friendly and serviceable dog; it would probably be impossible to do anything of the sort with the marsupial wolf. Nor do the instincts underlying family life, which are at the basis of so much of the latest developments of mind, seem to be well developed in mar-

supials; at least, a mother kangaroo, when hotly pursued, has been seen to eject her well-grown young from her pouch so as to help her own get-away.

The marsupial type, as we have described in Volume V of this Series, is a survival from the Cretaceous world of life, preserved by the accident of Australia's isolation. And in that isolation they seem to have made as little progress in brain-power as in method of reproduction. In other parts of the world the early placentals ousted and supplanted them; but the superiority of the victors seems to have rested in their new method of nourishing their unborn young rather than in their superior intelligence. Their brains in the early Cenozoic era were no larger or more elaborated than those of modern marsupials, and we may reasonably take the wallaby and marsupial wolf as giving an approximate picture of the behaviour of all the early Eocene mammals. Afterwards, the intenser competition in the broad spaces of the northern hemisphere put a premium on intelligence; and increase in brain-size became one of the salient features of mammalian evolution between Eocene and Pliocene.

Even so, some creatures with poor brains survived, either in out-of-the-way corners of the world, like the armadillos or sloths in South America, or in humble or obscure ways of life, like the shrews or moles. Such animals, it would seem, are almost on a par with lizards or birds as regards the automatic quality of their behaviour.

But as, during evolution, the proportionate size of the cerebral cortex was increased (a change visibly reflected in the foldings and convolutions of this outer layer of brain-tissue), the faculties of association and memory improved. All higher mammals learn well and rapidly. A dog knows his master, his friends, and his enemies; circuses would be impossible without the cleverness of elephants, horses, sea-lions and land-lions; the bears at the Zoo will gladly give you an exhibition of how quickly they can learn to manipulate such an unaccustomed object as a tin of treacle;

the foxes could not survive in the European countryside if they were not adaptable. But all this learning, however rapid, is, by our standards, of a restricted kind. It makes behaviour supple rather than truly intelligent. The performances of trained animals, and the tricks and much of the knowingness of our household pets, are deceptive because they are due very largely to the activities, deliberate or unconscious, of human teachers. The animals have been helped in their learning by man. Evidently the real test of an animal's intelligence lies in the things that it can find out of its own accord, without any assistance, and this is a matter which has only been investigated with scientific rigour in the last few decades. The method is to set a problem for the animal to solve, and then to see what it will do, taking the greatest care not to prompt or guide it in any way. If possible, the investigator should be outside the room and watch through a peep-hole.

A favourite type of experiment is as follows: Food is put inside a shut box, to which some latch or spring or hidden passage will give access, and the unfed animal is left outside the box; or vice-versa, the animal is imprisoned in a puzzle-box and food and liberty are outside. If practicable, the first method is the better, as the animals are not flustered or frightened at their imprisonment. Rats and squirrels can do little but find hidden weak spots through which they could dig a tunnel; but creatures with considerable skill in manipulation, like dogs and raccoons, are capable of quite elaborate feats. They learn how to slide back a bolt, to push down a lever, to pull the dragging-loop of a string which opens the door and so forth. They even learn, all by themselves, combination fastenings in which several operations have to be performed in a definite order before the door will open. But—and this is a very important point—they learn their tasks with scarcely an infusion of what one might call reasoning; the process is essentially one of trial and error. They claw about until a happy accident produces the right result; and then, as the test is

repeated, by what seems a fundamental law of learning, the successful movements are gradually "stamped in" to their behaviour, the unsuccessful one gradually "stamped out." They improve steadily in their performance until they do the trick quickly and automatically. But what they have mastered is a trick of movement, not an understanding of how the lever or the catch or the string works. They have not so much learnt a lesson as formed a habit. For alter the arrangement of the fastenings, without any change in the mechanical principle involved, and they have to begin again at the beginning with random scrabblings and build up a new movement-habit as laboriously as before.

A dog, for example, learns of its own accord to get into a large box for food, by pressing a little lever. One day the box is turned through a right angle. The animal is completely put off; it goes up to where the lever used to be and scratches away fruitlessly; and it takes as long to learn how to get in as it did the first time.

Just the same automatic habit-formation without any insight is brought about when animals are trained to run a maze to get food or liberty. Rats, for instance, will quite soon learn the secrets of even complicated mazes, such as a miniature of the celebrated one at Hampton Court. But this is a blankly unintelligent habit. A human being who has learnt a maze fairly well will never go wrong at the entrance; the first turning is the first thing he learns. But rats, even when they have reduced their mistakes to very few, are just as likely to make one at the first turning as anywhere else. Similarly, if a man is set to learn a maze which is a mirror-image of one he has already learnt well, he quickly recognizes the fact, and by always substituting right turn for left turn succeeds very soon with his new task. Not so the rats; such a maze is no easier to them than a completely new one. They are unable to grasp its analogy with the first.

We ourselves form motor-habits of much the same kind. Your house is, in a sense, a problem box; you have to learn

your way about it; and the mechanical automaticity with which you proceed from the bedroom to the dining-room to get your breakfast, perhaps while thinking of something quite different, is parallel to the mechanical way in which the animals solve their problems when they have been learnt. The animal sees its box, presses the lever, gets inside, and thus earns its meals; but it no more thinks out the train of actions as a logical sequence when it performs them than you think out the motions of your legs and the turnings of your door-handles on your way to breakfast. The process by which your motor-habit was established was rather different from the trial-and-error method of the animal, but the final result is strictly parallel. Another example of a human motor-habit is afforded by the actor who has repeated the same lines night after night for hundreds of nights, and now goes through his performance mechanically; if the habit, the automatic flow of words, should fail for a moment, he is helpless and breaks down completely.

It is not by any means easy to tell what part automatic motor-habits of this kind play in the lives of wild mammals. We may guess that a rabbit runs round its burrow as automatically as we run round our houses. In one or two cases, we have more definite information of animals whose actions have been stereotyped into a cast-iron routine. Thus there are animals which deposit their dung in the same place day after day, with extraordinary pertinacity. Then there are the rounds made by animals in search of food. The Malayan rhinoceros, for instance, has a regular round of feeding-grounds, which he covers in about a month. Dr. Ridley describes well-worn tracks through the forest, about three feet across, along which the animals travel, generally by night. There is a story of a temporary hospital hut, which had been hastily run up, and happened to be exactly on a rhinoceros track; when the beast came round again, he went in at one door, down the central passage between the beds, and out at the other, much to the alarm of the patients.

But we must get back to our puzzle-boxes. When a habit is established, its automatic execution is very similar in man and beast. But there is a great and important difference in the way in which habits are acquired. The animals in the experiments, in most cases at any rate, solve their problems by scrabbling about aimlessly and remembering the movements which happen to work. But put a man in a strange situation and the odds are he will behave in an altogether more reasonable way. He will think things over, and not begin to try solutions until he gets some kind of idea to work on.

We would make it clear here that the essential contrast does not lie between human behaviour and the behaviour of other mammals. It lies between two different methods of attacking problems. One method is to try all sorts of movements in the hope of muddling through; the other is to attempt to understand the problem before actually performing its solution. On the whole, most mammals in these experiments employ the first method, and most men, in the affairs of everyday life, employ the second.

Let us take a simple example. We rig up a little piece of wire-netting at right angles to the walls of a house; after three or four yards we put a right angle bend into it, so that it runs parallel with the house for another couple of yards. For our experiment with this simplest of "mazes" we choose three organisms—a hen, a dog, and a child of five or six. We lead them up to the wire-netting and throw a tit-bit (the tit-bit is, of course, suited to each subject) over it. The problem is successfully solved if the subject of the test without hesitation sums up the situation and makes off round the backwardly-projecting bit of wire-netting to the prize. You may say that the problem is so stupidly simple as to be no problem. Not at all. The hen never solves it properly. So long as it sees and wants the food it will dash and flutter vainly against the netting. If it does succeed in getting round to the tit-bit, it will be because it has abandoned the problem and started to go

away, and then accidentally turned so as to see the food from a more favourable position. The little human creature, on the other hand, will never fail to trot round. And the dog is intermediate. If the food is thrown well over the wire, the dog may make a few ineffectual jumps towards it, but then will, it seems, suddenly grasp the problem, and run round to get it in a purposeful and single sweep. But if the food be dropped just over the wire, so that it is within a few inches of its nose, it behaves as stupidly as the hen. The stimulus is now too potent; the dog is, as it were, magnetized by it and cannot acquire the detachment needed to run round; and so he remains scrabbling and barking stupidly at the unattainable food. Maier has studied behaviour of this sort in great detail. He finds it to occur also in other mammals, such as the rat. It is dependent on something akin to reason, and is quite distinct from the mere ability to learn a maze.

The differences in method of attack between bird, mammal and human child are impressive; they represent an important step in the evolutionary process that has led up to the human intellect. Let us summarize now the main stages in that process, as we have seen them.

First, is the completely unintelligent stage, when behaviour is inborn and stereotyped, and the individual has no power at all of profiting by experience but reacts like a machine to whatever stimuli may be acting at the moment. That stage we illustrated by considering in some detail the behaviour of the slipper animalcule. Confronted with a problem—such as a barrier across its path—this little automaton simply changes its direction at random and pokes about until it happens to get round.

Then comes the power of remembering which of a number of random responses happened to work in a given situation. This brings about a considerable economy of reaction; when the same problem confronts the organism again, it is solved in less time and with less expenditure of energy than before. Learning of this kind appears in a very crude

form in various invertebrates—we noticed it in earthworms (Chap. I, § 4)—and it runs through the vertebrate series. But it is always subordinated to instinctive reaction in animals below the mammalian grade.

Stage three is a further move in the same direction. The capacity of the cortex is extended; memories are accurately stored, and the power is acquired of comparing and contrasting different situations, of noting their resemblances, and of putting two and two together. Many mammals even have never reached this stage. It represents a further saving of effort and time; the dog which has learnt to open a puzzle-box and is then completely beaten when the box is turned through a right angle has to start again with random movements and gradually worry out a new solution. But a man who can look at the box and realize its change of position performs the appropriate movements as soon as that one thought-process is accomplished.

The performances of sheep-dogs show what the dog species can do when what is demanded is skilful adjustment of behaviour to a situation where essentials are already grasped; the experiments with wire-netting and puzzle-boxes show how limited is their power of thinking out the principles of wholly new situations.

Thus, with all their capacity for learning, most mammals do not seem to dispose of anything that merits the name of an idea. In the main, their learning powers are of our second grade above; they enable them to be steered into useful habits by a mnemonic selection of random movements. Their actions may look deceptively like our own—until suddenly some unexpected incident shows the profound difference. A cow, for instance, whose calf has been taken away from her seems as unconsolable as a human mother—but is wonderfully comforted by its stuffed skin.

Cases are on record where the mother, happily licking away at such a dummy calf, has licked its seams open, so that the hay with which it was stuffed has protruded; then it has proceeded to eat the hay. Ewes know their own

lambs—a remarkable feat of discrimination, one would think. But in reality, the recognition seems to depend on simple smell. Once the mother has licked her offspring, it is recognized as hers; if you substitute another lamb before her own has been licked, the changeling is licked and then treated as if it were the legitimate child. A rat, if the nerves of its foot have been severed, no longer recognizes this foot as part of its body, though it is still alive and pulsing with blood, but treats it as an extraneous object and proceeds to gnaw and eat it. It has no "idea" of its own body; and is normally prevented from maltreating its toes only by the pain which arises when they are nibbled.

And what of the dog, one of the more intelligent mammals, who still persists in burying bones, however well-fed, and in turning round and round before going to sleep as if the mat were herbage in which a bed had to be made?

This last example is a reminder of the importance which straightforward instinct still plays in the life of most mammals. Their instincts are much less fluid and command their lives much more directly than do ours; ours influence each other, become incorporated with ideas and modified by traditions, in a way which is new in life's evolution.

Miss Pitt, in her various books on natural history, has described how fox-cubs and young otters, growing up in captivity and free from the need of finding their own food, will suddenly reveal their latent instincts. Particular smells pull the trigger, and the hunting, pouncing, and worrying reactions, till then never exercised and never seen in others, are automatically released in full force.

The most remarkable mammalian instincts are undoubtedly those of beavers, who build dams and dig canals untaught. The dams serve to make pools in which they store food (bits of trees with the bark on them) and where there will be water under the ice in winter for them to swim to their food-pile. The canals are to facilitate their lumbering operations, when they have felled a tree and cut

it up into segments, it is easier to float them to the pond by water than to pull and push them overland. Dams may be up to a fifth of a mile long; and canals even longer. Both kinds of works seem to show engineering skill; the canals especially are run so as to ensure a gentle but unfailing flow of water. It is in the highest degree improbable that beavers have any comprehension of the principle of gravity or the fact that water finds its own level; exact observation will probably show that they regulate the course of their canals by some simple method of trial and error, such as only continuing to dig if the water flows, or is more than a certain depth. It is often stated that they fell their trees intelligently, gnawing at them so that they shall fall free and not be wasted by remaining entangled with other trees, but this appears to be a myth.

It would be a fascinating study for a student of animal behaviour to rear a group of young beavers by hand and discover exactly how much their unaided instinct was capable of; and still more fascinating if the group of untaught beavers could be compared with a group of untaught human children. But both experiments remain to be done.

It is a curious fact that the scientific mind and the activities of the reasoning faculty are so frequently written down as "inhuman." Actually this "cold" power of abstraction, this "inhuman" reason, is the one emergent property which the human species alone possesses, while our warm "human" emotions we share with the brutes. There can be no reasonable doubt that other mammals are subject to the same kinds of passions, feel the same sorts of emotion, as we ourselves. Our sheep can be frightened; our dog is glad when we come home, feels something closely akin to shame when caught in some misdeed; our cats can experience anger and disappointment. But the capacity to subtract eleven from twenty-four, to grasp that the earth is round and the sun some ninety million miles away, to understand general statements such as that Honesty is the Best Policy; to attach any meaning to abstract terms such

as Space or Truth—this is all distinctively and exclusively human. There are only the barest germs of such capacities in other creatures.

§ 7

The Springs of Action in Mammals

It is true, as we have seen, that very little of the behaviour of a mammal is wholly instinctive. Almost invariably it is in some degree learnt. But all that learning and experience can do is to modify something already given. And it remains true that the fundamental motives to action are given by heredity. The central core of instinct remains as an emotional urge or drive: it is the methods by which the drive is translated into action which are learnt or modified by experience. Any young mammal has to learn what is good to eat and how to find it: but it does not have to learn to be hungry.

Heredity, we may say, prescribes some general end—the satisfaction of hunger, thirst, sexual desire, the need for escape, and so on: the animal depends to a greater or lesser degree on learning to find out how best to attain that end.

These inborn urges towards various biologically important goals are generally styled *drives* in modern psychological parlance. They are accompanied by strong feeling, and constitute the inner springs of action.

With some of the more elementary drives, we already know something of their physiological basis. The sensation of hunger, for instance, with the accompanying urge to eat, depends upon contractions of the muscular walls of the stomach. Thirst depends largely upon the dryness of the lining of the mouth: a man who has just drunk his fill can be made violently thirsty again by a blast of dry air in his mouth. With other impulses, however, such as gregariousness in social creatures, we are quite ignorant of the underlying mechanism.

Various experimental procedures have been adopted in

order to measure quantitatively the strength of a drive and its variation with time, and to compare the intensity of different drives. A simple one is to record the number of revolutions of a revolving wheel, such as one used to see in squirrels' cages, where alone the animal can take exercise. Using this method, it was found that female rats became much more active during each recurring period of heat, relapsing into comparative sluggishness when the sex-urge disappeared. But this cannot be used for elaborate or comparative experiments.

The best method so far devised seems to be that of Professor Warden of Columbia. The animal to be tested is placed in a cage containing two compartments joined by a passage. In the connecting passage is an electric grid which gives disagreeable but not injurious shocks when the animal enters it from the first compartment. At the end of the second compartment is placed a reward—food, if the hunger-desire is being tested, a female for the male sex-drive, a young animal for the maternal drive, and so on. The strength of the shock is kept constant, and the number of crossings made in twenty minutes is taken as a measure of the drive's intensity (the animal is of course not allowed to satisfy its hunger or other urge until the end of the experimental period).

With rats as subjects, it was found that for all drives the intensity would rise for a period until it reached a maximum, and then fell off, even for elemental needs like food or drink. The order of intensity of the various drives, measured by their maximum, was not what most people would expect: the maternal instinct headed the list; then came thirst, with hunger close behind; and then sex, with an intensity less than two-thirds of that of maternal instinct. The urge to exploration, as tested by providing a network of alleys, the inquisitive rat being allowed to penetrate a little further each time, was less than half as intense as sex. It is perhaps remarkable that it is sufficiently developed to force the animal to brave an unpleasant shock six times in twenty

minutes: even a rat is endowed with the beginnings of scientific curiosity.

Wiesner tried another method of measuring the strength of the maternal urge in rats. He found that the stronger it grew, the older were the young animals which the mother rat would retrieve, and the more curious the substitutes for her rightful offspring. A very motherly rat will retrieve half-grown rats, chickens, or even young kittens nearly as big as herself. Nor is the maternal drive easily satisfied. The same experimenter tested one animal which retrieved over 500 young rats in quick succession, piling them all in one great heap.

Obviously researches of this sort, though as yet they have touched only the fringe of the subject, will lead on to important results. They will make it possible to measure the ebb and flow of the tides of what we loosely call our energy, and understand the way which it is dependent on outer stimulus and inner physiological state. It is no good having in your brain the most efficient mechanism for intellectual processes or aesthetic creation if you lack the driving force to keep them at work. The drives, in ourselves as in other animals, are the power machinery: it is off their main shafts that the detailed machines of thought and action are driven.

§ 8

Education in Animals

The higher vertebrates, we see, can learn, mammals much more than birds. The development of the brain and especially of the cortex means the progressive replacement by flexible responses of the fixed responses of an instinctive system. Putting it compactly, the purely instinctive animal is born complete; the higher animal is born incomplete and learns. And it is advantageous therefore that the protective association of parent and offspring so characteristic of the higher types should involve a certain assistance in

the learning process. This assistance is the beginning of education.

Not all animals that learn, educate. For education, family or community life is one necessary pre-requisite. Birds like the bush-turkeys of Australia, in which eggs are buried in mounds of earth and left to develop by themselves, hatch out away from all parental care, and have to rely on their own innate machinery of response from the very start of their lives. Obviously no education is possible to such a type. And in many other birds, even though family life is developed and the parents feed and protect the young, nothing occurs that one can really call education. Mechanical responses of offspring to parent are not education. The crouching of young birds at their mother's warning call does not have to be learnt; it is an automatic and innate response, like the blinking of our eyelids to a threatening hand. According to Hudson, unhatched birds that are squeaking while still inside the egg will stop their noise at their parents' alarm-call. The small part which training plays in bird life is brought home forcibly by the familiar fowl with her foster-brood of ducklings, who, one fine day, all untaught and very much to the distress of their acting parent, proceed to swim away across a neighbouring pond.

Flying again is an activity as innately given as swimming; when the time comes and the muscles and nerves are developed to the proper pitch, a bird will fly; it will fly a little awkwardly at first, and practice will be needed to give it full mastery of the air, but it has no need of any training to be able to use its aviation machinery without danger of crashing. Most young birds take their first flight quite independently of their parents; but in some species the old birds, though they are in no way concerned with helping their young to greater skill, as a golf or a skating instructor helps his pupils, still assume the definitely educational task of stimulating the young bird to take the plunge at the earliest possible moment. Some eagles, for instance, when the young have been five or six weeks in the nest, no longer

feed them so regularly; after a time they may withold food altogether, but will sit about in the neighbourhood of the nest, calling, until the young birds grow bold through hunger and launch themselves into the air. It has even been stated that old birds will take their young on their backs and then sweep downwards, leaving them to fly as best they may; but this is probably a traveller's tale. Curiously enough, although ducklings will go to water of their own accord, young gulls and swans have to be brought there and induced to enter the strange element.

Many birds of prey, however, plainly educate their young in hunting. Falcons catch and cripple prey and then leave it to be finished off by their offspring, just as many beasts of prey bring home wounded animals for their half-grown young to try their claws and teeth upon. Grebes let their children pursue fish which they have caught and liberated again in a damaged state. In many cases the mother helps to teach the children what kind of food to look for; the clucking of a hen attracts her chicks to come and see the morsel she has found. Even if the parents do not impart instruction so deliberately, the mere existence of a family group constantly puts the young in situations where they must profit by their elders' experience of the world. Lion-cubs, when they are big enough, are taken on their parents' hunting expeditions, and it is stated that they do not become independent hunters until they are over eighteen months old.

Just how far these cases represent a true handing-on of actual experience from old to young is difficult to determine. We have seen that in most mammals, and probably all birds, learning consists in making more or less random movements, without any definite purpose behind them, and retaining those of them that are found to be useful. The parents, in the examples which we have discussed, do not so much present their young with the results of their experience as help them to get experience for themselves. They hurry the normal process up: that is all. The kitten con-

fronted with an injured mouse examines it, plays with it, claws at it, and so learns how to handle it in much the same way as it would learn how to solve the riddle of a puzzle-box; the mother cat, by bringing the mouse, has provided opportunity but not direct instruction. The education is essentially self-education.

One commonly hears it said that parent animals teach their young by doing things in front of them which the young try to imitate. But in actual fact, it is very doubtful whether any mammals, other than monkeys and apes, have a sufficiently well-developed imitative faculty for this. In experiments with puzzle-boxes it was often noticed that if animals saw one of their fellows press the right lever, or had the human experimenter repeat the trick a dozen times before their eyes, they learnt nothing from it. Even if they were held and passively put through the trick themselves, it was rarely of any avail; the movements, to be learnt, must be their own. In our own species, any modern educationalist will tell you how much better children remember what they have done or been persuaded to do of their own initiative.

In monkeys and apes and ourselves, the instinct to imitate brings about a great abbreviation of the educational process, by leading the young to make only those movements that they will find to be profitable. But how far this occurs in other mammalian species is still doubtful.

The greatest extension of the educational process came with the invention of language; for this made it possible for the actual experience of one generation to pass on to the next. Not only this, but contemporaries share their experience. "I don't advise you to buy such-and-such a make of car," says Jones to Brown. "Robinson got one, and it's rotten." By means of the written and spoken word, the joint experience of millions of living beings rolls up into a single whole.

Nowhere else in the mammals is this handing of experience from the individual who has experienced it to one

who has not, even paralleled. But there is a somewhat analogous case in birds.

It has been known from time immemorial that not only parrots but many birds will imitate the sounds they happen to hear. To this, the mocking-bird owes its name; the American blue-jay, the European starling and sedge-warbler imitate other species in a state of nature, while raven and mynah can readily be taught new notes in captivity. Bullfinch fanciers train their prize birds by the aid of a pipe to whistle special phrases, and then the birds are made to sing against each other in public.

Of late years, critical investigations have revealed the surprising fact that whereas in some birds the song is entirely inherited, so that young males raised out of earshot of their own kind (and even forced to hear the songs of other birds) will in due course give the characteristic song of their species, in others the full song must be learnt, and isolated males never get farther than a few notes or feeble phrases. An experimentally-minded German fancier has even succeeded in grafting the nightingale's song on to a strain of canaries. The young canaries were reared in a soundproof room where the only singing birds were cock nightingales, and the nightingale's short song-period was supplemented by gramophone records through the winter. The canaries picked up the alien song; and now, after a few years, this has become self-perpetuating, since the cocks sing only nightingale-wise, and their offspring learn from them. The song is not exactly like the nightingale's, for the tone-quality is shriller, the phrasing not quite perfect; but it is far more nightingale than canary. In such species, song (like human language, but unlike the croaking of frogs or the music of grasshoppers) has to be learnt anew in each generation.

But in general, education, even in the warm-blooded birds and mammals, plays only a minor rôle. It is one of the latest tools of life, whose more elaborate possibilities, latent from the time when men began to speak, are only beginning to be exploited.

This is, perhaps, the place to speak of the various animal prodigies, the calculating horses and conversational dogs, who have made their bow before the public in the last thirty years. (It is interesting, by the way, how such phenomena come and go in bunches; they seem to be catching, or at least there are fashions in them. This has been true for mesmerism, for table-turning, and for various aspects of spiritualism.) The claim is made (large books have been written about it) that horses, for instance, can be trained to perform quite complicated arithmetical calculations, and that Airedale terriers can discuss morality and a future life with their mistresses. Since animals lack the power of vocal speech, their utterances have to be conveyed by movements, generally of the feet. The commonest method is that employed in table-rapping; so many taps with the right foot means such and such a letter or number; with the left foot, they mean some other letter or number.

The calculating horses of Elberfeld attained such a celebrity that solemn commissions of university professors were appointed to consider their case. Their portentous arithmetical capacities and the equally supernormal (but rather banal) communications of the philosophical terriers have provided much helpful material for theosophists and spiritualists.

But in sober truth, these thinking horses and dogs do not reflect at all deeply. What the creatures invariably do is to notice and respond to little signs given by their masters or mistresses. Sometimes the signs have been given deliberately; but in the great majority of cases there is no deception and the movements are unconscious—slight gestures, a shift of the head, a twitch of a finger, unconscious movements of the same kind as those which are utilized by the professional "thought-readers," who, though their eyes are bandaged, find a hidden object by holding the hand of someone who knows where it has been hidden. They may be all but unnoticeable by the human observers—movements through a twentieth or a fiftieth part of an inch; but the animals, who do not have to keep their attention on the talk, can spot them.

The dog or the horse goes on tapping the ground with his foot until he sees the movement which he takes as the sign to stop; then he stops. It is worth mentioning that the horses often do not even look at the black-board on which the problem is chalked up, before beginning the tapping. Also that the errors which they most frequently make are not in the least the sort of errors one would expect, like a failure to carry ten; usually the mistake consists in being one wrong in the answer—tapping twenty-two instead of twenty-one, for instance, or else in transposing digits and tapping twenty-seven, say, instead of seventy-two. In the former case they have not noticed the movement until just too late; in the latter, they have used the right foot in place of the left—that is all.

§ 9

Play

Play is so ingrained in human life that we rarely trouble to ask ourselves how it originated and what its meaning may be. The children of Greece and Rome had their dolls and toys; so did those of Ancient Egypt, twice as far back in time, and so, we may safely hazard, did the children of the later Old Stone Age. And if the children had their playthings the parents had their games; one of the recent discoveries at Ur, dating from over 5,000 years ago, was a board for some sort of game resembling draughts.

But play is rare in other than human life. With the possible exception of ants, play is unknown outside the vertebrates; and among vertebrates, it is not certainly known outside the two warm-blooded groups, the birds and mammals. If the bird attains the highest level of courtship, it is the mammal which best knows how to play.

What is the biological function of play? Let us consider a few examples to clear our minds about this question. We are standing in the bows of a steamer in the Mediterranean. Some distance away we see a series of leaping forms,

one behind the other, each curving over in a semicircle to dive below the surface and re-emerge a few seconds after. They are a file of dolphins. After a time they sight the ship, and alter their course to meet it. Then the real fun begins. They play around her stem, never actually achieving contact with her sides, yet always on the verge of it. Now one of them bores down into the blue water until he is a mere dim shadow; now he comes twisting up again. Sometimes they circle right round the ship; but usually they are content to gambol around the bows, effortlessly keeping up with the power-driven machine. Only after hours will they leave her.

No fish would ever behave like this. Fish will leap out of the water, but only to avoid their enemies; they will keep poised in the current of a stream, but only because that is the business of their lives. The dolphin and the porpoise are mammals; and they prove it by their playing. Those who prefer everything to be sensible and simple have suggested that porpoises really frequent the bows of ships to rub barnacles and other encumbrances off their backs; but the unanimous verdict of those who have watched them is that this is not so—the porpoises are not being reasonable, they are being playful. Sometimes this play-impulse may be linked up with others; porpoises may play round ships not only because they like playing but because they anticipate scraps being thrown overboard.

Kittens are perhaps the most playful of all young animals. Everyone knows how a kitten will spend minutes intently patting a cotton reel or a rolled-up scrap of paper across the floor, how a dangled string or watch-chain will lure him on, how he will pounce in pretence at hands moving under the coverlet, or even pursue his own tail in ludicrous gyration. Gradually this playfulness will die out, and the kitten give place to the staid cat who prefers dignified fireside purring to the frivolities of play. Most adult cats preserve only one play-activity; they play with the mice they have caught, letting them go to recapture them a hundred times before they finally kill them.

Kittens, as befits the offspring of a solitary species, are perfectly contented to play alone; but puppies, though they are by no means averse to solitary sports, such as worrying an old boot to bits, play best in company. On such occasions the make-believe and pretence which characterize so much playing, animal as well as human, is vividly revealed. Two half-grown pups are playing at fighting; they rush at each other, roll over and over, snap, growl, worry. And yet neither ever hurts the other; they always know when to stop. They are not angry; but they are thoroughly enjoying themselves playing at being angry. And in just the same way they will indulge in mimic chasings, first one and then the other taking the rôle of pursuer.

Birds, like mammals, will play. The snake-bird or darter is a fresh-water cormorant with amazingly long and flexible neck, by whose aid it pursues and catches agile fish under water. A female snake-bird has been seen sitting on the swamp-cypresses in a Louisiana pond and playing at catch, all by herself. Reaching down with her long neck, she picked a small twig, then threw it up in the air and caught it in her beak. This was repeated until she misjudged matters and missed the twig; she cocked her head at it as it fell, and proceeded to pick another with which to continue the play.

In birds, the commonest form of play is flying play. Ravens, in spite of their size and staid appearance, have various aerial sports. A favourite one is to turn almost completely upside-down in the middle of ordinary flight, giving a hoarse croak at the critical moment; this may be repeated over and over again. Or they may dive and somersault together in the breeding-season. The small egrets and herons that nest here and there in protected rookeries along the coast of Louisiana and Texas return every evening to their breeding-pond from feeding on the marshes. A steady concourse pours in, along various flight-lines, about 200 feet up. Arrived above their home, they simply let themselves drop. Their plumes fly up behind like a comet's tail, they scream with excitement, and when not far above the ground,

spreading the wings so as to catch the air again; they skid and side-slip wildly before alighting.

Now we can begin to say something more definite about play—what it is and what it is not, its occurrence, its meaning. Play occurs in adult as well as in young animals. Usually it is described somewhat obscurely as an outlet for surplus energy. But such activities as the cat's playing with mice are definite responses to particular situations, and the downward plunging of home-bound egrets and herons could equally well be described as a way of achieving a necessary action in the most pleasurable and exciting way. Whether or not it serves to excrete surplus energy, the play may take very various forms. It may be a direct imitation of some regular activity of the species, but playfully carried out, like the sportive fighting of dogs, or the cat's behaviour with captured mice. Though not a complete imitation, it may be obviously connected with some such special activity, as is the pouncing of the kitten ; or it may serve to use some special activity in a new and interesting way, as in the snake-bird's twig-catching play. Or again, it may serve the same end for some more general activity like bodily movement ; and in such case, the surplus activity may simply overflow in sheer exuberance, as in the romps of young lambs or puppies, or be guided into more special and fixed channels, as in the somersaulting of ravens. The same differences are to be seen in our own play. Many games are more or less accurate imitations of serious activities, others are mere romps ; and there are sports which, like ski-ing, we practise mainly for their thrills of new and violent bodily motion ; there are adults' games which go back to the playfulness of childhood. There are many children's games which anticipate the business of later life :

> Behold the child among his new-born blisses.
> A six years' darling of a pigmy size . . .
> See, at his feet, some little plan or chart,
> Some fragment from his dream of human life
> Shaped by himself with newly-learned art.

From the point of view of its evolution and its biological

meaning, play seems to have a double origin. There is the play which is biologically useful as a preparation for adult life; this is play in the strict sense. And there is the play which results from a mere surplus of energy being directed into pleasurable or exciting outlets; this, if we want to distinguish it, we can call sport. The former is more characteristic of young animals, the latter of adults; the former predominates in the mammals, the latter among birds. Karl Groos, in his classical book, *The Play of Animals*, stressed the view that play is essentially useful to the species; and that, since it was useful, its origin could be accounted for on ordinary selectionist principles. Others have preferred to believe that play was wholly useless, and could be accounted for altogether as an aimless overflow of energy. But our distinction between preparatory play and sportive play enables us to take a middle course.

Preparatory play is found almost exclusively in mammals. It depends on the fact that a mammal comes into the world as a singularly unfinished product. Most of us do not realize how much we had to teach ourselves in our childhood. Avoiding objects as we walk about, judging distances, picking things off a table—all such acts are so automatic to us that they seem trivially simple. Yet we had to learn them all, and the learning of them was one of the most elaborate of our acquisitions. As a reminder of what that learning meant, we may describe a striking experiment carried out by Professor Stratton on himself. He had spectacles made which inverted everything: when he put them on, the world was upside-down to him. He wore them continuously and naturally had to learn how to fit his movements to this new picture of his surroundings.

> When I saw an object [he writes] near one of my hands and wished to grasp it with that hand, the other hand was the one I moved. The mistake was then seen, and by trial, observation, and correction the desired movement was at last brought about.

It took him several days before he could begin to work smoothly in the new conditions. Even more difficult (per-

haps because it looked less queer) than the inverted world was a world produced by another set of glasses in which right and left were transposed, as in the world we see in the looking-glass. With these glasses, " At table, the simplest act of serving myself had to be cautiously worked out " ; and it took him a week before he had adjusted himself fairly adequately to this mirror-image world. On the eighth day he removed the glasses—and by then the new habits had become so well learnt that it took him over twenty-four hours to get back to normal. The effect of a week's reversal of right and left was strong enough to override the habits of a life-time and for a day to keep him very literally " out of touch with reality."

An insect, because of the stereotyped elaboration of its nervous system, can fly as soon as its wings are dry and stiff, and not only so, but it can direct its flight in relation to other objects. But the mammal has to learn how to control its limbs, and how to correlate movement with sight. Its mental peculiarity necessitates a period of playful immaturity.

This is why the higher mammals, with their greater brain-power and capacity for learning and their longer infancy, excel in preparatory play, while the birds, which become adult in a few weeks, and are less intelligent, play very little when they are young. But in sportive play the birds, with their high temperature, ceaseless activity, and wonderful bodily powers of flight, excel the mammals, who tend to become more lethargic as they grow up ; only a few mammals, like some seals and porpoises and dogs and monkeys and apes, go on playing all their life long. Whales may leap bodily out of the water ; and probably this is a form of sporting thrill. The two forms of play, of course, grade into each other. The exercise of twig-catching skill by the snake-bird helped, no doubt, to keep her hand in (or rather her neck) for the business of catching fish, and the flight-sports of birds must keep their powers in trim against the serious tests of gales and storms. None the less, the distinction is a useful one.

To what a pitch pure sport may go in birds is shown by the community flying-games of rooks. Here is a typical observation. A large gathering of these gregarious and intelligent birds was seen in a field in February. About half the birds were excitedly walking about and cawing; others were mounting in steady spiral flight, all fairly close together. When they had arrived at a height of four or five hundred feet, one after another they folded their wings and dropped. They whizzed down like plummets; when only forty or fifty feet from the ground they spread their wings and began braking with them. As a result they skidded and swerved through the air in the wildest way, eventually alighting to walk about and caw a little before repeating the sport. The sport itself is like that of the egrets; here, however, it is not merely an embroidery of the necessary return to their homes, but is organized for its own sake, as we laboriously plod up hill with toboggan or skis in order to enjoy the downward rush. The same sort of sport has also been observed in early autumn; and once, it is recorded, the rooks were seen to mount so high that they disappeared from sight; only then, at several thousand feet up, did they turn, dropping out of the blue to attain alarming velocities before they put on their brakes. As sensational and as clearly practised for sheer enjoyment is the behaviour recorded of snipe—not the species as a whole, but a few sporting individuals—in flying upside-down. In the most remarkable case, a snipe which had been "drumming" up aloft came swooping down, and when only a few feet above the ground turned on its back and continued, thus inverted, in a horizontal course for several hundred feet.

Perhaps the most human of all cases of animal play is one recorded by Levick for Adelie penguins. Floes and little bergs of ice were all the time drifting in a strong current past the edge of the land where their rookery was situated. The penguins loved to take joy-rides on these. They swam out and leapt up, until the ice-platform was sometimes too crowded to take another bird. They drifted down, con-

tentedly, excited, for about a mile; and then swam up again to take a fresh ride.

Probably similar to the rooks' aerial sports are the dance-gatherings of some other birds. Jaçanas, according to W. H. Hudson in his *Naturalist in La Plata*, assemble in bands and dance and scream, meanwhile waving their wings, whose brilliant yellow is usually hidden. And our stone-curlews assemble, after the breeding-season is over, to indulge in the strangest antics, flapping, rolling sideways, racing about. From these primitive dances it is not a long step to

FIG. 40.—ADELIE PENGUINS AT PLAY—TAKING A RIDE ON A DRIFTING ICE-FLOE.

(*Courtesy of Dr. G. Murray Levick, from "Antarctic Penguins," Heinemann.*)

the choral performances of another bird studied by Hudson on the pampas, the crested screamer. Although these are big, heavy creatures, a large flock of them often circles up until lost to sight, and there, in the upper air, the birds begin a melodious trumpeting, which floats down to the hearers below with more than the mystery of the hidden choir in Wagner's *Parsifal*.

Such community-singing is not uncommon, though in a less romantic setting, among song-birds. Although that migratory thrush, the redwing, only breeds in the far north of

Europe, yet before they leave their winter quarters in England, considerable flocks of them may assemble in trees and give a concert, which, since the full song is not yet developed, is strangely subdued in its effect. These breed gregariously; but even in solitary nesters like the European goldfinch, such concerts may be given in early spring when the urge to song has begun to be felt, but the birds are still in flocks and bands.

Birds that roost communally often carry on the most animated "conversations" morning and evening at their roosting-places. Rooks are a familiar example: starlings are still more striking. Of late years starlings have taken to sleeping in huge numbers, not only in the trees of London squares, but on the City buildings. It is one of the most remarkable experiences to hear the thousands of starlings on the cornices of St. Paul's Cathedral begin to sing and chatter at dawn in autumn, long before the City's population has arrived. The volume of sound is enormous; for a time the birds merely converse, but soon a few begin taking little flights from place to place on the building; the flights become longer and more numerous; and after twenty minutes or so bands begin to leave in all directions for the business of the day.

An even stranger preface to the day's work has been observed with swallows and martins. If you get up at dawn on a fine morning, somewhere where there are a number of house-martins' nests still unfinished under the eaves, you will probably see no birds about. They have all flown up many hundreds of feet into the air, as if to greet the rising sun as early as possible. When the rays of the sun touch them, their little twittering band sinks slowly down with the sunlight; and they begin their ordinary activities when they are down again to earth.

Certain animal habits are more like obsessions than play. Creatures that collect stores for the winter, for instance, often amass much more than they can ever use. The passion for collecting takes them, and they lay up food like a miser

hoarding gold. Such animals as squirrels bury their food-stores in little caches here and there; and perhaps the majority of these hiding-places are permanently forgotten. The squirrel who makes many food-caches and forgets most of them is in its way like the fish or the sea-urchin who produces huge numbers of young only to have the great majority die early. The system is a wasteful one, like so many of nature's systems, but it works because enough of the caches are rediscovered, just as the sea-urchin's reproductive methods work because the survivors, though few, are enough. The squirrel's habits, however, may benefit the plants whose seeds he stores; he often provides for their dispersal, and by burying and then forgetting them, he puts them into the best condition for germination.

The passion of certain birds, notably those of the crow family, for bright objects is well known; though magpies are really the most thorough-going performers, literature has made the Jackdaw of Rheims the best-known example. We do not know how this behaviour has originated; probably it is a combination of a hoarding instinct with an appreciation of brightness and striking colour. It is at any rate certain that quite a number of birds have a simple fondness for things that are to us striking or pretty, and use them to embellish their nests in the same way as we call in the decorator as well as the utilitarian builder when we are building houses. Birds of prey, such as buzzards and eagles, break off branches of greenery to put round their nests, renewing them as they fade. A number of wading birds put shells or bright pebbles round the depression which serves for their eggs; an interesting point in many of these species is their variability—some individuals decorate their nests abundantly, others sparsely, still others leave them bare. A queer case is that of some of the American flycatchers, who always hang a cast-off snake-skin on their nest—whether to decorate it or to protect it is quite unknown.

Levick found that Adelie penguins loved bright colours. The sitting birds are always stealing stones from each others'

nests; Levick accordingly painted a number of stones with different colours, and put them within reach of the birds at one edge of the rookery. They were much coveted, and by repeated thieving, travelled steadily across the colony. He made the interesting discovery that red stones travel the fastest. Although red is a colour which the penguins can seldom see in their normal environment, it tickles their senses as it does ours.

§ 10

The Behaviour of Monkeys and Apes

The construction of apes is so like our own that their actions constantly remind us of familiar human doings. We see an ape mother fondling her baby, and it seems to us that she must be experiencing the feelings appropriate to a human mother; we see a sad-faced orang-outang in a cage, and his expression convinces us that he is thinking about his past life, free in the Bornean jungle, as a human prisoner would think of his lost liberty. But then something happens that gives us pause. The orang mother wants to travel from one end of the cage to the other. The baby that her arm has been encircling at her breast is shifted to her prehensile foot and is bumped over the floor as she swings herself arm over arm along the roof-bars; she does not look nearly so human now. Or the melancholy philosopher in the corner —if he is thinking, why does he never talk? If he is so human, why does he suddenly break off into some unrepressed obscenity? Is the mind behind the actions really so like our own?

Curiously enough, it is only in very recent times that any systematic study of ape behaviour has been made. Just before the War, the German psychologist Koehler made a notable beginning on this problem, studying the behaviour of a group of young chimpanzees, four to seven years old, some fresh from the wild, and none previously trained in any way, in the warm climate of Teneriffe. The Americans,

headed by Yerkes, have since then made intensive studies of various apes, and so has Mrs. Kohts in Moscow.

How like are these creatures to ourselves? That is the fascinating problem in all these researches.

On the emotional side, there is a very strong resemblance. One need not be an expert observer to tell by looking at its face what a chimpanzee is feeling; its series of emotional expressions is almost identical with our own. Weeping,

FIG. 41.—EXPERIMENTING WITH CHIMPANZEES.
Mrs. Kohts testing her chimpanzee Ioni in the matching of colours.
(*Courtesy of Mrs. Kohts, Moscow.*)

perhaps, has a rather unfamiliar look, and the pursed and protruded lips of excitement so much exaggerate the thrilled child's gesture when it says "Oo-ooh" that the grimace seems unnatural and grotesque. But they fondle their babies and kiss their friends, human as well as simian, to show their affection in an entirely human way. They obviously like play for its own sake, especially when young, and are human enough to enjoy teasing other and stupider creatures like fowls.

When it comes to more complex feelings, the resemblance continues. Jealousy they share with many of the tailed monkeys, such as baboons. Madame Abreu, a Cuban lady, whose large collection of apes and monkeys on her estate

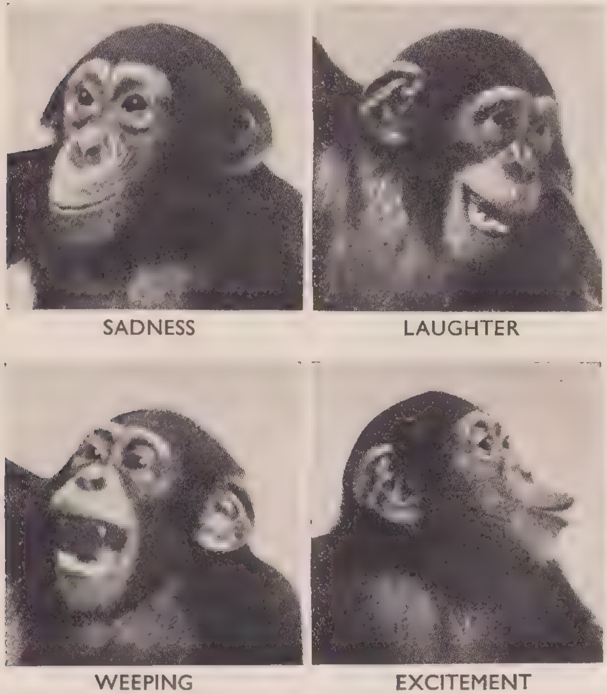


FIG. 42.—ANTHROPOID EXPRESSIONS.
Mrs. Koht's chimpanzee Ioni, moved by various feelings.
(*Courtesy of Mrs. Kohts, Moscow.*)

in Havana has been studied and described by Yerkes in his book *Almost Human*, had a baboon who always tried to hide his mate when any male human being came near the cage ; women, on the other hand, he did not worry about.

Madame Abreu once brought a Catholic priest as test-object to see if the baboon would take him for a woman on account of his long cassock; to judge by his behaviour he was not deceived.

Curiously enough, although callousness and indeed brutality are often manifested by chimpanzees, sympathy also is strongly developed in them. If one of their group is ill, he will not be teased or disturbed; now and again one will come over and caress the ailing companion. Actual whimperings or moans of pain will almost invariably bring the other chimpanzees round a sufferer, often with touching manifestations of concern; but Koehler found that ape-sympathy, though so readily expressed, needs stimulation. Out of sight, out of mind; when he removed sick chimpanzees to a distant hut, the others betrayed no recollection of them—they neither searched for them nor showed any signs of sadness or feeling of loss. Much the same is true of their affection for their babies. When a baboon or a chimpanzee baby dies, its mother generally refuses to part with its corpse, but carries it about until it becomes dry and mummified. Tricks have to be resorted to to get the body away. But once it is gone, memory is short-lived; after a little searching, the mother shows no sign of remembering her loss. In this, as in so much else, the ape's behaviour differs from ours chiefly in respect of its immediacy.

The chimpanzees are among the most sociable of animals. The greatest punishment you can inflict upon a young chimpanzee is to put him into solitary confinement. He pines, mopes, grows listless and sickly. They are almost as ready to accept companionship from human beings as from their own kind; but now and then explosive happenings remind the human that he is dealing with a different species of organism. Koehler, for instance, in his *Mentality of Apes*, forcibly describes the working of their herd instinct.

> The moment your hand falls on a wrong-doer, the whole group sets up a howl, as if with one voice. . . . At times the most insignificant episode between man and ape, which arouses a cry of anger against the

enemy and springing against him, is sufficient for a wave of fury to go through the troop ; from all sides they hurry to a joint attack. In the sudden transfer of the cry of fury to all the animals whereby they seem to incite one another to ever more violent raving there is a demonaic strength. It is strange how full of moral indignation this howling of the attacking group sounds to the ears of man ; the only pity is that every little misunderstanding will call it forth as much as a real assault ; the whole group will get into a state of blind fury, even when most of its members have seen nothing of what caused the first cry, and have no notion of what it is all about.

Fear, too, can be induced. If Koehler went into the cage, simulated terror and looked fixedly in one direction, the chimpanzees ran together and looked fearfully in the same direction, although of course there was nothing whatever to be frightened of.

In such a socialized animal, the instincts of self-suppression and self-assertion are of great importance. One outcome of the self-suppressing tendency is seen in the trustful way in which many chimpanzees submit themselves to medical treatment. An outcome of the urge to self-assertion is the immediate advantage which they take of the least weakness or timidity in other apes, or in human visitors. And the interplay of the two opposed tendencies results in the establishment of a regular order of precedence. After a group of them have lived together for a week or so, each will have found his social level. One (who may be of either sex) will be head of the gang ; and of the rest each will boss certain individuals and let himself be bossed by others, without matters ever coming to a head in a fight.

Individuals of other species of monkey and even human beings may be drawn into the network of precedence. De Haan records an amusing instance of how this system works with tailed monkeys. He was experimenting with a mangabey and a macaque. The mangabey entirely dominated his companion ; he had only to lift his eyebrows or show the whites of his eyes for the macaque to throw down his food and retreat hurriedly into another compartment. The mangabey, on the other hand, felt himself inferior to the

man. He offered no resistance to De Haan's threatening gestures or looks, but reacted to them in a regrettably human fashion (very like that of the clerk who has been hauled over the coals by the manager and vents his spleen on the office-boy), by looking viciously at his companion, who immediately slunk off into the small compartment.

One day, De Haan wanted to demonstrate this procedure to the keeper. But now when he threatened the mangabey, it sprang at him instead of turning on the other monkey. To the monkeys, the keeper was a much more important personage than the man of science; and the fact that he was there and remained benevolently neutral was sufficient stimulus to the self-assertive side of the mangabey to make him react directly to De Haan's threats; but as soon as the keeper left the room, the mangabey gave up his bold face. If the keeper threatened the monkey and De Haan stayed quiet, the beast turned on De Haan; but if De Haan came with a visitor and made threatening gestures, it was the visitor who was treated as an inferior and snarled and screamed at. If De Haan pretended to have a scrap with another man, the mangabey always took sides; and he always sided with the "higher in rank"—with De Haan against a casual visitor, but with the keeper against De Haan. As our author says: "It was certainly surprising and somewhat disappointing to see how this feeling of the rank of the different persons predominated over sentiments of personal affection."

We could run on and fill a chapter with details of the emotional behaviour of monkeys and apes, so fascinating are its odd resemblances and differences to our own. But the reader can go to the admirable books of Yerkes, Koehler, and Zuckerman; for our present purposes a few more anecdotes must suffice.

A young orang-outang whom Yerkes was testing would show his discouraged puzzlement with a problem that was too much for him by repeatedly bumping his head none too softly against the floor, just as a man might hit his head with his fist in despair at his own stupidity.

An adult male chimpanzee at Madame Abreu's place began to evince an embarrassing interest in a fair-haired girl in the kitchen whom he could see at her work from his cage. The door into the kitchen was accordingly screened; and the chimpanzee saw the screen being put up by one of the men attendants. Before this, the man who had been instrumental in depriving the chimpanzee of the sight of the blonde kitchen-maid had been on very friendly terms with this chimpanzee; but a few days later the ape, seizing his opportunity, made a vicious attack on him. The complex feelings engendered by this incident prevented the ape ever afterwards from looking his former friend in the eyes, or even accepting food or caresses from him.

Large and unfamiliar animals produced panic in Koehler's chimpanzees. The sight of two big oxen so terrified them that it acted like a purge; and the passage of a camel made it impossible for any experiments to be done for a considerable time.

Koehler then undertook some experiments with crudely-stuffed toys. The realistic school of animal psychologists would have us believe that animals are only likely to react strongly to an object which is familiar or at least pretty similar to something in their natural environment.

> But [he writes] the chimpanzee's reactions were in almost comic contradiction to this view. Almost any representation of an animal, even if small and friendly-looking, is treated as uncanny; and larger and more grotesque toys are the occasion for paroxysmal terror.

When Koehler came into the cage carrying a goggle-eyed quadruped, about eighteen inches high, with some resemblance to a donkey, " in a second a black cluster, consisting of the whole group of chimpanzees, hung suspended in the farthest corner; each tried to thrust the others aside and bury his head deep in among them," and when he suddenly put on a Cingalese devil-mask, the apes were equally terrified.

It was the combination of resemblance and difference that inspired their terror. Purely geometrical constructions had no such effect as animal toys, and merely concealing the face

in a sheet would not act as did the mask. This encourages us to believe that the lantern-bugs (discussed in the section on Mimicry, in the Sixth Volume of this Series) which look like miniature reptilian heads, do profit by the resemblance; and also gives us an insight into human nature. The uncanny, that which inspires with awe and sacred terror, is not the completely strange; if it is too far beyond ordinary experience it is simply not grasped. To be effective, it must combine the familiar with the unfamiliar; it must be strange, but recall what is well known. It appears, by the way, that chimpanzees and other anthropoids may recognize their own species in a film, and also dangerous objects such as snakes.

Let us come now to the intellectual development of the ape. Here the difference between apes and men is more marked—and this in spite of the apes' conspicuous superiority over other mammals. They have no true language; that is their first and greatest deficiency. They have a rich and varied vocabulary of sounds, and these are often used for communication; but they are always expressions of their feelings, never descriptions of objects. If a chimpanzee has a banana taken from him, he can express the fact that he is angry; if he wants a banana, he can express the fact that he is hungry; if he gets a banana, he can express the fact that he is satisfied. But he cannot say anything about the banana itself. No ape has any words for things. Nor is it easy to train apes in language habits. With great difficulty, one chimpanzee has been taught to use a few real words; other experimenters have failed to achieve even this much.

Their mental life extends very little either into the future or the past. Like young children, they live mainly in the present. There are many stories, apparently well-authenticated, of apes attacking the author of some injury after months of absence; and we are apt to think that this implies a memory like our own. But there is no evidence that the creature has any power of mental recall. The offender has generated resentment against himself; when he shows him-

self again, resentment is again aroused. This is an example of a long-enduring effect of past experience; but that is no evidence that apes (or any other animals) can be human enough to brood over their injuries, or think revengefully of an absent enemy.

In what way, then, are the apes on a higher level of behaviour than cats or dogs or horses? In considering this question, we must bring in the tailed monkeys, since in brain and behaviour they are half-way between the tailless primates and the other placentals. The first characteristic of the higher primates' behaviour is their manipulative restlessness. They are always inquisitively exploring their environment, always enjoying themselves by doing something with their hands. They are much better acquainted with the varied objects around them than are any other creatures. These monkey tricks are the foundation on which human science and industry was finally erected. Confronted with puzzle-boxes and similar problems, monkeys seem little more intelligent than other mammals. But they have a greater range of movements, and they are undoubtedly more imitative, though not so imitative as popular belief would have them.

Their quickness and restlessness seem not to be particularly useful to them; it is rather an overflow, a by-product of their active arboreal life. Their lack of concentration prevents them turning their capacities to service.

The tailless apes are a stage higher. For one thing, they are more imitative; for another, they have more insight. The surprising tricks which apes can be deliberately taught are only of secondary interest. It is remarkable that chimpanzees can be trained to have as good table manners as many children; that they will learn to dress and undress themselves; that they will even sign their names (Consul, the famous performing chimpanzee, had his own banking account and signed cheques on it). But all these are only evidence of the apes' manipulative skill and docility. Consul, we can unhesitatingly affirm, had no idea that the marks he made on the paper were his name, or the least notion of

what a cheque was; he had been taught a trick, like a dog that does "*Trust and Paid for.*"

What really interests us is their level of intelligent insight. Koehler tried to find out what untaught chimpanzees could achieve by putting food out of their unaided reach, at the same time providing simple implements by which, if they were clever enough, they could reach it. Throughout, the greatest care was taken that no human being should give the apes any hint of what implement to use or how to use it.

The chimpanzees succeeded in accomplishing the following feats. They realized that they could use sticks to beat down a banana hanging from the roof, or to reach one on the ground outside the cage. Once they had learnt this, they learnt to break off branches to use when no sticks were handy. They employed bigger sticks as vaulting-poles to leap at suspended food. If a string which they could reach was tied to food which they could not reach, they at once pulled the thread towards them (a feat of intelligence that sounds simple, but is probably quite beyond a horse or a cat). To catch ants (which they liked eating for their acid flavour) outside their cage, an ape would poke a straw among the ants until they crawled on to it, then pull the straw back and lick the ants off it. They used a hanging rope to swing on and so clutch a suspended banana. They used packing-cases, big stones, or even people to climb on and reach up to fruit. Most interesting of all, they could combine implements. One animal saw how to fit one stick into another to make the long implement he needed. They also piled two, three, and sometimes even four packing-cases on top of each other when more height was necessary.

Thus they have, it is clear, a considerable power of solving simple mechanical problems; and they usually solve them, not by blind trial and error, but with the aid of what we have called insight—either solving them outright or by trial and error illuminated by some understanding of the situation. Later research has shown that tailed monkeys, including some of the less developed South American type, have a much

FIG. 43.—AN ANTHROPOID ENGINEER.

One of Koehler's chimpanzees has discovered how to pile three boxes on top of one another to secure a banana. The construction has proved adequate, but is rather insecure. Note the sympathetic movement of the spectator's left hand. (*From Prof. W. Koehler's "Intelligenzprüfungen an Menschenaffen" ("The Mentality of Apes"), by permission of Julius Springer of Berlin and Kegan Paul, Trench, Trubner & Co., Ltd., of London.*)

Fig. 44.—The Use of Implements by Apes.

A young and untrained chimpanzee, using two packing-cases to stand on, employs a long pole to knock down suspended food.

(From Prof. W. Koehler's "Intelligenzprüfungen an Menschenaffen" ("The Mentality of Apes"), by permission of Julius Springer of Berlin and Kegan Paul, Trench, Trubner & Co., Ltd., of London.)

greater capacity of insight than used to be supposed. None the less, the apes appear definitely to out-distance all other animals in this respect.

An amusing experiment on the mental powers of chimpanzees has recently been carried out at Yale. They were provided with a penny-in-the-slot machine in which the insertion of a poker-chip would reward them with some grapes. When they had learned the use of this, they would willingly do heavy work on another apparatus to get tokens, which they would then convert into grapes in the first machine. Even if they were forced to wait an hour before "cashing in," they would work hard for the chips; and, still more remarkable, when chips of two different colours were used, one of which secured them twice as much fruit as the other, they soon learned to work for the more valuable token. Thus they can learn to appreciate the value of objects that are useless except as tokens for something they want, just as we learn to appreciate the token value of such an intrinsically worthless object as a banknote.

But the chimpanzees' limitations are quite as striking as their achievements. In Koehler's experiments, they had only the feeblest insight into mechanics. Their towers of boxes were usually unstable. They could never see that a ladder was safe when it made an angle with the ground, but persisted in pushing it with one side right up against the wall, and its rungs accordingly at right angles to the wall—with the result that it fell over when they began climbing up it. If their rope was wound round a beam in three turns, not even overlapping, they never could see how to begin unwinding it, but pulled haphazard at it like a man confronted with a vast insoluble tangle of string. When given the choice of pulling two strings, one of which was attached to a banana, while the other merely lay close to it, they almost invariably pulled the string that ran straight towards the fruit, irrespective of whether it was fastened to it or not; it seems very dubious whether apes have any understanding of the mechanical situation which we call connection of string and object.

They very rarely thought of using an implement which was out of sight. Usually the stick and the food had both to be visible for the ape to think out the connection between them.

Many other facts could be cited to show that their insight, though it takes them farther than any other animals, fails before situations which to us appear laughably easy. Their limited association-centres will not allow them to grasp many elements in one act of thought.

And their average powers as a species are much lower than we have implied. For it is by no means all of them which can solve such problems. Individual chimpanzees differ as much, both in temperament and intelligence, as human individuals. Many remain baffled, or sulky, or complacently unsuccessful; the more difficult problems were never solved, or even repeated, by any save rare ape-geniuses. Perhaps the most interesting of all the many interesting things that wait to be done in biology would be to take a group of clever chimpanzees and see what could be accomplished by fifty generations of selective breeding for intelligence. They are so near the critical point at which language and abstract thought begin; could one help them across it?

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